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J. B. THOMAS
Forest Insect Laboratory
Sault Ste. Marie, Ontario

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The Use of Larval Anatomy in the Study of Bark Beetles (Coleoptera: Scolytidae)¹

By J. B. THOMAS²

INTRODUCTION

During recent ecological investigations of bark beetles in coniferous trees in Eastern Canada, the need for a key to the identity of bark beetle larvae became apparent on numerous occasions when larvae of more than one species were found in the same area of bark, or when adults had emerged leaving immature forms only. A review of the literature in this connection did not provide a solution, revealing instead that there were relatively few classifications of species of Coleoptera using larval characters, even in part, compared with those based entirely on imaginal characters. MacGillivray (1903) published a key to the larvae of some of the more common families of Coleoptera, and a more comprehensive one to the larvae of most families of Coleoptera was published by Roberts (1930). The illustrated key to the principal larval forms of the order by Böving and Craighead (1931) is an excellent treatment of this subject. Larval keys to families of beetles of the British fauna were published by VanEmden (1942). Peterson (1951) published the results of his study of larval Coleoptera, his revision of Robert's key resulting in a form more satisfactory than the original for North American species. While identifications are to families only, the book is profusely illustrated with diagrams of many species of each family featuring their diagnostic characteristics. Böving (1954) published a description of the external anatomy and musculature of larvae of the family Anobiidae followed by an interesting discussion of the taxonomic characteristics, including a key to species.

Classifications of species of Scolytidae have usually been based on imaginal characters, a number of the most important contributions being those of Hopkins (1909, 1915a, and 1915b), Blatchley and Leng (1916), Swaine (1918), Dodge (1938), Chamberlin (1939), and Beal and Massey (1945). Hopkins (1905) stated that larval characters refer the species of *Dendroctonus* to practically the same positions as had the adult characters, and may indicate closer natural affinities. In 1909, he attempted one of the earliest classifications of bark beetle larvae, including in his treatise on the genus *Dendroctonus* a separation of the species based on larval characters. Gardner (1934) published the preliminary results of his work on scolytid larvae, with keys to certain genera and species found in India. It was intended primarily for identification, and detailed descriptions of some genera and species were presented. Other references in the literature to scolytid larvae are concerned mainly with descriptions of isolated species. Of these, a few are very useful for comparative studies of individual species. Russo (1926) published an account of the biology and morphology of *Chaetoptelius vestitus* Fuchs, introducing a system of nomenclature for the setal patterns on the head and body. The morphology of the genus *Gnathotrichus* Eich. was described by Schedl (1931), but his discussion of the larvae was restricted to one species, *G. materiarius* Fitch. A detailed description of the larva of the native elm bark beetle, *Hylurgopinus rufipes* (Eich.), was published by Kaston (1936).

Since no publications dealing specifically with larval identification were found, larvae from known adults of the following 30 species of bark beetles, representing 15 genera, were examined with the primary object of determining

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²Forest Insect Laboratory, Sault Ste. Marie, Ontario.

whether larvae could be identified to genus or to species. These are listed according to the arrangement given by Chamberlin (1939):

Subfamily Hylesiniinae

<i>Crypturgus atomus</i> Lec.	<i>Dendroctonus simplex</i> Lec.
<i>Polygraphus rufipennis</i> (Kby.)	<i>Dendroctonus valens</i> Lec.
<i>Dendroctonus piceaperda</i> Hopk.	<i>Phloeosinus canadensis</i> Sw.
<i>Dendroctonus rufipennis</i> (Kby.)	<i>Hylurgops pinifex</i> (Fitch)

Subfamily Scolytinae

Scolytus piceae Sw.

Subfamily Ipinae

<i>Trypodendron lineatum</i> (Oliv.)	<i>Pityophthorus consimilis</i> Lec.
<i>Gnathotrichus materiarius</i> (Fitch)	<i>Pityophthorus nudus</i> Sw.
<i>Conophthorus coniperda</i> (Sz.)	<i>Pityophthorus puberulus</i> Lec.
<i>Conophthorus resinosae</i> Hopk.	<i>Pityophthorus pulchellus</i> Eich.
	<i>Pityophthorus</i> sp.
	<i>Pityophthorus</i> sp.
<i>Pityogenes hopkinsi</i> Sw.	<i>Pityokteines sparsus</i> (Lec.)
<i>Pityogenes plagiatus</i> (Lec.)	<i>Orthotomicus caelatus</i> (Eich.)
<i>Ips borealis</i> Sw.	<i>Dryocoetes affaber</i> (Mann.)
<i>Ips calligraphus</i> (Germ.)	<i>Dryocoetes americanus</i> Hopk.
<i>Ips chagnoni</i> Sw.	
<i>Ips perturbatus</i> (Eich.)	
<i>Ips pini</i> (Say)	

As the study progressed, it became apparent that more than the minimum objective of identification might be achieved, and the comparative anatomy of the larvae was then considered for possible taxonomic and phylogenetic relationships. While the number of species available for study has not been extensive, the preliminary results appear sufficiently promising for presentation as an indication of possible affinities between genera, which can be the subject of further critical study. These observations may stimulate searching reviews of existing classifications based on adult characters alone, and comparative studies of a wider range of species may promote the development of a classification utilizing both larval and adult characters.

TECHNIQUES

Anatomical characters useful for taxonomic purposes are only valid, of course, if they have been found from an examination of known larvae. A number of precautions were taken in assembling the larvae used in this study to ensure that they were the progeny of adults that could be or had been identified. Larvae collected from isolated galleries in which the parent beetles were still present, or from those in which the parents were absent, but part of the brood had developed to the adult stage, or larvae reared from known parents were used for the most part. Some species were received from collectors who were certain of the identification of the parents and from reference collections of various laboratories and museums.

Few bark beetle larvae are large enough for detailed examination in comparative studies without mounting the head capsule, mouth parts, and body on microscope slides. The following techniques were developed in this study using larvae preserved in 70 per cent alcohol, and have proved very satisfactory. With the larva held ventral surface up (jeweller's hair spring forceps are very suitable), a cut was made with a fine scalpel between the mandibles and the

combined maxillae and labium, and was continued around the edges of the occipital foramen, thus separating the head capsule, with the mandibles, from the body. The maxillae and labium, still attached to the anterior edge of the prosternum, were then removed as a unit. Bodies of large specimens could be examined after removing the internal tissues without dissecting them further. In most cases, however, it was necessary to dissect the integument and mount the pieces. Bodies of two specimens were used; the first, after decapitation, was cut through the pleural regions ventral to the spiracles; the second was cut through the mid-dorsal and mid-ventral regions. In this manner, one dorsal, one sternal, and two pleural sections were obtained with the setal patterns undisturbed.

The body, entire or sectioned, one head capsule, and the maxillae and labium were placed in a 10 per cent solution of KOH for sufficient time to loosen the muscles and connective tissues. The time required to do this varied with different specimens, correct timing being learned with experience. Best results were obtained when whole or sectioned bodies were removed from the KOH solution before the turgidity of the integument was completely gone to prevent the walls from collapsing as the muscles and other tissues were being removed. Loosened muscles, connective tissues, and internal organs were removed with forceps and dissecting pins, or were flushed out using a fine glass syringe. The mandibles, with attached tendons, were removed from the head capsule with forceps. The clypeus, labrum, and epipharyngeal lining were left attached to the head capsule in some cases; in others, they were removed and mounted separately to permit more detailed examination.

The foregoing preparatory steps for the head capsule and mouth parts were frequently avoided by the selection of specimens that were moulting or pupating, or had just completed pupation. In these, the head capsule had split into a frontal and two parietal sections along the ecdysial suture, and could be removed from the head or the next-instar larva or from the pupa, entirely free of muscle tissue. Complete head capsules could be obtained if the old capsules were removed after the exoskeleton of the next-instar larva or pupa had formed but before splitting had occurred along the ecdysial suture. If pupation was complete, the shrivelled-up last larval skin frequently adhered to the posterior abdominal spines of the pupa, and mouth parts and sections of the head capsule could still be obtained.

Parts of the body were overstained in Gage's acid fuchsin, usually for 20 to 30 minutes, and then immersed in a 10 per cent solution of KOH for one or two seconds. This appeared to remove all the stain, and the KOH, which formed a white precipitate in the Hoyer's solution used as a mounting medium, was in turn removed by washing for a few minutes in water or alcohol. Some of the stain re-appeared when the sections were placed in the mounting medium, this technique producing better stained specimens than were obtained by a light, initial staining only. Hoyer's solution was more suitable than Canada balsam as a mounting medium, since specimens could be mounted in it directly from either water or alcohol of any concentration. Where large head capsules were mounted, the cover slips were supported on chips of glass to prevent crushing, or hanging-drop slides were used. Specimens to be examined under phase contrast were mounted in the same manner, but staining was unnecessary.

Some of the drawings were made with the use of a squared Whipple disc inserted in the eyepiece of a binocular or compound microscope. Many drawings, however, were traced from images of mounted specimens projected through a compound microscope on to a frosted glass plate. When the image was sharply

focussed, a tracing was made directly on engineering tracing paper. Details were later completed by examination of the specimen through the microscope.

THE EXTERNAL ANATOMY OF A TYPICAL BARK BEETLE LARVA

Larval description of species examined in this study, and of additional species as they become available, will be published following this introductory paper to provide the basis for further comparative studies. To establish a standard nomenclature for this and future papers and, at the same time, assist readers who may not be familiar with bark beetle anatomy, the setal nomenclature to be followed, and the external anatomy of one species, *Hylurgops pinifex*, selected as typical of the larvae of most species of bark beetles, has been described in the following sections.

Setal Nomenclature

Russo (1926) developed a system of nomenclature for the setae on the head and body of one species of bark beetle, *Chaetoptelius vestitus* Fuchs, which was adopted and modified by Schedl (1931) for use in describing the setal pattern of *Gnathotrichus materiarius*. Russo gave individual names to most of the setae on the head and mouth parts, but named only groups of setae on the thorax and abdomen. Schedl's modification consists of a reduction in the number of names by giving names to distinctive groups of setae and numbering the setae within a group, at the same time latinizing the Italian names. The name used is descriptive as to position on the head or body, e.g., seta frontolateralis, indicates one of a group of setae on the lateral region of the frons. Kaston (1936) adopted Schedl's new nomenclature in his work on the morphology of *Hylurgopinus rufipes*, modifying it where necessary to conform to differently interpreted morphology. On the other hand, Hopkins (1909) discounts the value of the setae in the descriptive anatomy of *Dendroctonus valens*. Anderson (1947), working with the closely allied larvae of Curculionidae, has developed a nomenclature for the setal pattern of the head and body. The setae on the head are numbered and referred to as frontal, epicranial, or clypeal, depending upon their location. The epicranial setae are further subdivided as to position, that is, dorsal, ventral, lateral, or posterior. The setae on the thorax and abdomen are numbered and identified by reference to the particular lobe or fold of the segment on which they are located. Setae on the mouth parts have been identified as labral, epipharyngeal, mandibular, maxillary, or labial.

The nomenclature used in this paper in describing the setae of scolytid larvae is a modification of Anderson's system bearing in mind the different group of insects being studied and a different interpretation of certain parts of the external anatomy. The names applied to various setae or sensilla, or to groups of these, indicate to a certain degree the general location of each on the body. In certain groups of setae, the relative position of setae within the group is indicated by the use of numbers after the name applied to the group and, of course, is contingent upon a specified direction for the numbering. For groups of setae in which no orientation of individuals is evident, only the total number comprising the group is given. The evident similarity in the anatomy and setal patterns of larval Curculionidae and Scolytidae has influenced the selection of a system of nomenclature that will permit some comparison of their respective setal patterns. In this study both names and numerals are used for comparative purposes only. While giving the same number to a seta in a corresponding position in different species may infer homologies, these have not been studied.

Names of setae and sensilla found on the head capsule, mouth parts, thorax,

and abdomen of scolytid larvae are listed below together with the abbreviations used in illustrations.

Head Capsule:

Pes	Posterior epicranial setae	Fig. 6
Des	Dorsal epicranial setae	Fig. 6
Les	Lateral epicranial setae	Figs. 6, 7
Ves	Ventral epicranial setae	Fig. 7
Fs	Frontal setae	Fig. 6
Clps	Clypeal setae	Fig. 8
Desl	Dorsal epicranial sensilla	Fig. 6
Lesl	Lateral epicranial sensilla	Fig. 7
Vesl	Ventral epicranial sensilla	Fig. 7
Pesl	Posterior epicranial sensilla	Fig. 6
Fsl	Frontal sensilla	Fig. 6
Clpsl	Clypeal sensilla	Fig. 8

Labrum and epipharyngeal lining:

Lms	Labral setae	Fig. 8
Ams	Anteromedian setae of epipharyngeal lining	Fig. 16
Als	Anterolateral setae of epipharyngeal lining	Fig. 16
Mes	Median epipharyngeal setae	Fig. 16
Esl	Epipharyngeal sensilla	Fig. 16
Lmsl	Labral sensilla	Fig. 8

Mandible:

Mds	Mandibular setae	Fig. 12
Mdsl	Mandibular sensilla	Fig. 12

Maxilla:

Sts	Stipital seta	Fig. 9
DLcs	Dorsal lacinial setae	Fig. 10
VLcs	Ventral lacinial setae	Fig. 9
Mxps	Seta on maxillary palpus	Fig. 9
Pls	Palpiferal setae	Fig. 9
Stsl	Stipital sensillum	Fig. 9
Plsl	Palpiferal sensillum	Fig. 9
Mxpsl	Sensilla on maxillary palpus	Fig. 9
VLcsl	Ventral lacinial sensillum	Fig. 9

Labium:

Plbs	Postlabial setae	Fig. 9
Prbs	Prelabial setae	Fig. 9
Lis	Ligular setae	Fig. 9
Lisl	Ligular sensilla	Fig. 9
Pmtsl	Premental sensilla	Fig. 9

Thorax and Abdomen:

1Ts	Prothoracic dorsal setae	Figs. 1, 2
2TIs	Mesothoracic dorsal setae, fold I	Figs. 1, 2
2TIIs	Mesothoracic dorsal setae, fold II	Figs. 1, 2
3TIs	Metathoracic dorsal setae, fold I	Figs. 1, 2
3TIIs	Metathoracic dorsal setae, fold II	Figs. 1, 2
Als	Abdominal setae, fold I, segments 1-8	Figs. 1, 2
AIIs	Abdominal setae, fold III, segments 1-8	Figs. 1, 2
9As	Dorsal setae, 9th abdominal segment	Figs. 2, 4
10As	Anal setae	Figs. 3, 4
DPls	Dorsopleural lobe setae	Fig. 2
VPls	Ventropleur lobe setae	Fig. 2
Ps	Pleural setae	Fig. 2
Sps	Spiracular setae	Fig. 2
As	Setae of alar area, mesothorax and metathorax	Fig. 2
Msts	Mediosternal setae	Figs. 2, 3
Lsts	Laterosternal setae	Figs. 2, 3
Sts	Sterna setae of 9th segment	Figs. 2, 3
Peds	Pedal setae, thoracic segments	Figs. 2, 3

External Anatomy of *Hylurgops pinifex* (Fitch)

The body is apodous, and is curved dorsally into a shallow crescent shape characteristic of most species of bark beetles. The head is hypognathous and amber, with the mandibles and epistomal region brown to black and the remainder of the body a creamy-white. Each thoracic and abdominal segment is composed of a number of integumental folds, not separated by distinct sutures, which give the larva a wrinkled appearance (Figs. 1, 2, and 3). Each thoracic segment bears on the ventral surface a pair of lobes having a sclerotized area set with setae. In addition to these lobes, which may be used in locomotion, the greater part of the surface of the integument is covered with fine, backward projecting, cuticular spines, which are probably of considerable assistance in locomotion and in anchoring the larva in the larval mine. The head, thorax, and abdomen bear a number of setae.

Head

The head (Fig. 2) is normally retracted toward the prothorax, thereby concealing the narrow band of cervical membrane. The head capsule is slightly longer than wide, and the sides are sub-parallel continuing into a broadly rounded caudal region. The cranium is divided by the Y-shaped ecdysial line into a frontal and two parietal areas. The stem of the Y is the coronal suture (Fig. 6), which appears double for that part of its length where it parallels the midcranial inflection. The frontal sutures, forming the arms of the Y, proceed latero-ventrally ending at the membranous areas around the bases of the antennae (Figs. 5 and 6). The midcranial inflection is apparent internally as the midcranial apodeme (Fig. 7) and externally as the endocarinal line extending part way into the frons (Fig. 6). While there is no distinct epistomal suture, the anterior edge of the frons is more darkly pigmented, and is inflected to form the epistomal apodeme (Fig. 16). The lateral angles of the epistomal area, on each side of the clypeus, are produced anteriorly to form the dorsal articulatory processes of the mandibles (Figs. 5, 6 and 7). A suture proceeds posteriorly from the point where the outer edge of the dorsal articulation of the mandible meets the basal membrane of the antenna, toward the frontal suture (Figs. 5 and 6). Internally, there is a corresponding apodeme continuous with the epistomal apodeme and at right angles to it. From the position of the internal ridges, the external line, which is indistinct, is interpreted as the frontogenal suture with the corresponding frontogenal apodeme. Hopkins (1909, Fig. 40E) has indicated the presence of this suture in his drawing of the head of the larva of *Dendroctonus valens*, but has not named it. Schedl (1931) and Kaston (1936) did not describe such a suture in the larvae of the genus *Gnathotrichus* and of *Hylurgopinus rufipes*, respectively.

The edges of the oral foramen are thickened and inflected from the antennae to the ventral articulations of the mandibles forming a strengthening rim, the subgenal inflection (Fig. 5). Continuing posteriorly, the rim of the oral foramen remains inflected forming an internal ridge from the ventral articulation of the mandibles into the gena for a short distance (Figs. 5 and 7). Adopting Snodgrass' (1935) name, the hypostoma, for the sclerite cut off from the gena beyond the posterior mandibular articulation, this ridge is called the hypostomal apodeme. Outwardly the ridge is marked by the hypostomal suture, and a hypostomal lobe projects into the foramen at the point of articulation of the maxilla (Fig. 7). The postocciput is a slightly inflected, narrow rim of the occipital foramen cut off by the postoccipital suture (Fig. 7), and posteriorly it is continuous with the midcranial apodeme. The neck membrane is attached

along the line of the postoccipital suture. The tentorial bridge, apparently formed by the fusion of the posterior tentorial arms, forms a strong support between the sides of the head (Figs. 5 and 7), and separates the oral and occipital foramina. There are two projections on the posterior edge of the bridge to which muscles are attached. The anterior tentorial arms arise internally from points at the anterior edge of the frontogenal sutures, proceed posteriorly for a short distance parallel to the inner surface of the frons, and then are connected by slender ligaments to the anterior edge of the posterior tentorial bridge (Figs. 5 and 7). The anterior tentorial pits are not visible. A ligamentous rod connects the opposing sides of the ventral edge of the oral foramen directly posterior to the ventral, articulatory processes of the mandibles (Figs. 5 and 7). This is the hypopharyngeal bracon which supports the hypopharynx.

The number and arrangement of setae and sensilla on the head capsule are indicated in Figs. 6 and 7. In the following description, the numbers quoted are for the setae and sensilla located on one-half of the head capsule only. Since the setae are seen to best advantage when the head capsule is mounted on a slide, the positions of the setae have been given with the head capsule in a prognathous orientation which places the actual anterior surface in a dorsal position. The frons bears five setae, numbered 1 to 5, beginning at 1 and proceeding anteriorly to 5 located at the anterior end of the frontogenal suture. Numbers 1 and 2 are alongside the endocarinal line with a single sensillum located about midway between the two. Number 4 is anterolateral to 2 in the anterior half of the frons, with 3 lateral and posterior to 4. A second sensillum is located close to seta 4.

One pair and a group of three setae located on the parietal region are called the dorsal epicranial setae (Fig. 6). Number 1 is mesial to 2 about one-third the distance along the vertex of the epicranium beyond the posterior limit of the frons, with 1 nearer the coronal suture. The group of three setae is located lateral to the frons in a triangular formation with 3 close to the frontal suture, 4 lateral to 3, and 5 anterolateral to 4. Three sensilla are associated with the dorsal epicranial setae (Fig. 6). Sensillum 1 is posterior to seta 1, sensillum 2 is usually slightly posterior to seta 1 but may lie very close and lateral to it between setae 1 and 2. Sensillum 3 is located approximately on a line between setae 3 and 5.

A row of four very minute setae, posterior epicranial setae, (Fig. 6) begins posterior to dorsal epicranial seta 2 and proceeds posteriorly, curving mesially. A single sensillum is located outside of this row near posterior epicranial seta 2 (Fig. 6).

A pair of setae, located near the anterior region of the head capsule and lateral to the anterior group of dorsal epicranial setae, is referred to as lateral epicranial setae, number 1 being farther back (Figs. 6 and 7). Two sensilla are associated with these, one between the two setae and one posterior to seta 1 (Fig. 7).

The final pair of setae are minute, located on the ventral side of the head capsule posterior to the ventral articulation of the mandible (Fig. 7). Ventral epicranial seta 1 is the more posterior of the pair. A single sensillum is located posterior to seta 1 (Fig. 7).

The clypeus is a broad sclerite hinged to the anterior edge of the frons (Figs. 6 and 8) with angular sides and a broadly emarginate anterior margin. A pair of setae is located on each side of the clypeus, anterior to the frontoclypeal suture, with a single sensillum close to each pair of setae but slightly anterior in position. The inner of these two setae has been numbered 1, the outer, 2.

Mouthparts

Labrum and epipharyngeal lining: The labrum is a broad sclerite, narrower than the clypeus and movable on it by the clypeo-labral suture (Figs. 5, 6, 7 and 8). The anterior margin, the median part of which is produced slightly, folds under and is continuous with the membranous inner lining of the labrum and clypeus (Fig. 16). The posterior edge of the labrum is drawn out into a point extending below the clypeus, and is visible externally as a more darkly pigmented area. Attached to the anterior, inner surface of the labrum are two sclerotized rods, the tormae (Figs. 8 and 16), the free sections of which extend posteriorly, gradually approaching each other until, in some cases, a weak line of fusion occurs between the posterior ends. The labrum bears two groups of three setae (Fig. 8). A single sensillum occurs in the centre of the labrum and a second sensillum is located laterad of seta 1.

There is no epipharynx in the sense in which the term was first introduced into insect morphology, but rather there is a membranous epipharyngeal lining of the labrum and clypeus extending into the oesophagus. The membrane is supported by the tormae and bears three distinct groups of setae. A median pair of setae is located on the anterior edge of the epipharyngeal lining, and a second group of three setae is located anterolaterally of the base of each torma (Fig. 16). Setae of both of these groups are stout and well developed. Three pairs of short setae are located between the tormae (Fig. 16). Also, there are two pairs of sensilla, in clusters of three on the epipharyngeal lining, one pair on either side of the posterior pair of setae (Fig. 16).

Mandible: The mandibles are short, stout, and heavily sclerotized, the dorsal or outer aspect being slightly convex as opposed to the concave ventral or inner aspect. The cutting edge is sharp and bears three distally placed incisoral teeth as well as a much smaller tooth located about midway between the third incisoral tooth and the base of the mandible (Figs. 11 and 12). The outer, posterior angle of the base of the mandible bears a large, rounded condyle which articulates with the ventral articulatory process of the head capsule. The mandible articulates dorsally with the articulatory process of the head capsule situated lateral to the base of the clypeus. The contraction of the abductor and adductor muscles, acting in a plane at right angles to the axis of the mandibular hinge, operates the mandible. The muscle tendons are shown in Figs. 11 and 12, the inner, adductor tendon being much larger than the abductor. The mandible bears two small setae on the outer surface in a vertical alignment, and three sensilla, two at the base of the mandible on the outer surface, and one mesad of the setae toward the cutting edge (Fig. 12).

Maxilla: The maxillae are situated alongside the labium and are membranously united with it as seen in Fig. 9. The cardo is a distinct basal sclerite broadly hinged to the base of the stipital region and articulating with the maxillary condyle of the head capsule. The body of the maxilla is composed of the fused stipes, palpifer, and lacinial lobe, none of which are delimited by sutures. The palpus is two-segmented with the basal segment set in a membranous area of the palpifer. The first segment of the palpus bears a minute seta and two sensilla while the distal segment bears a single sensillum and a number of apical papillae. The lacinial lobe bears a row of seven long, stiff setae on the dorsal side, and a group of five setae plus a single seta and sensillum on the ventral side (Figs. 9 and 10). The outer margin of the lacinial lobe adjacent to the palpus is more heavily sclerotized and may represent the vestiges of the galea, a theory held by Hopkins (1909) concerning a similar area in the larva of *Dendroctonus valens*.

A long seta is located near the base of the stipital area with a sensillum posterior to it, and two long setae are borne on the edge of the basal membrane of the palpus with a sensillum between the two.

Labium: The labium consists of two parts, the postlabium and the prelabium. The postlabium as described here corresponds to the submentum in *Gnathotrichus materiarius*, *Hylurgopinus rufipes*, and *Dendroctonus valens* described by Schedl (1931), Kaston (1936), and Hopkins (1909) respectively. Similarly, the prelabium, which consists of a strongly sclerotized, trident-shaped, premental sclerite, palpigers, palpi, and a median ligular area, corresponds to the mentum described by the same authors.

The postlabium (Fig. 9) is a broadly rounded, semi-membranous, basal segment connected ventrally to the prothoracic sternum and laterally to the maxillae, and bears two groups of three setae numbered consecutively from the posterior to the anterior end. The three setae of each group are arranged in the form of a triangle with 2 closer to 3 than to 1, and lateral to both.

The prementum has a distinct, posteriorly projecting, median arm and three anterior arms. A pair of sensilla is located on the sides of the prementum directly below the base of each lateral arm, and at the distal end of the anterior median arm. A long prelabial seta is located in each U-shaped area between the median and lateral arms.

The palpi are 2-segmented; the distal segment is narrower than the basal and bears a number of apical papillae. Each segment bears a sensillum on the ventral side.

The ligula, forming a median semi-membranous lobe between the palpi, bears four short setae anterior to the median arm of the prementum. One sensillum is located on either side of the two anterior pairs of setae.

Hypopharynx: The hypopharynx is a fleshy lobe forming the floor of the mouth cavity, continuing into the oesophagus (Fig. 15). The distal portion, formed of a leathery membranous tissue, has a concave outer surface and appears as an inner reflection of the ligula of the labium. The lateral areas bear many cuticular spines while the proximal portion is a sclerotized sheath partially encircling the oesophagus. The hypopharynx is supported by the hypopharyngeal bracon (Figs. 5 and 7).

Thorax and Abdomen: The body of the scolytid larva is divided into three thoracic and ten abdominal segments, with the tenth abdominal segment represented indistinctly by anal folds (Figs. 1, 2, 3, and 4). The segments are delimited by intersegmental lines or grooves rather than by membranous conjunctivae separating definite sclerotized segments.

Dorsum: There is a tendency, evident from a review of the literature, to apply the names of sclerites, which have been developed in specific cases to meet specific needs, to other non-homologous areas of the larval insect body. To cite a few examples, Hopkins (1909) used the terms prescutum, scutum, scutellum, and postscutellum to indicate integumental folds developed in response to the pull of segmental muscles in the dorsum of the larva of *Dendroctonus valens*. Böving (1914) adopted Hopkins' terminology so far as it applied to campodeiform larvae, and later used it in descriptions of the larvae of beetles of the subfamily Galerucinae and the family Cleridae (Böving, 1929b, Böving and Champlain, 1920, respectively). Craighead (1915, 1916 and 1924) continued the use of this terminology in describing cerambycid larvae. Roberts (1926) has designated areas of the dorsum in the abdomen of some weevil larvae as

prescutum, scutum, and scutellum, and Schedl (1931) and Kaston (1936) have followed a similar course in their work with scolytid larvae.

Much of the confusion in terminology arose from early attempts by workers to prove that each segment of the thorax was composed of four distinct rings or subsegments. The number of segments believed to have formed the thorax ranged from two to twelve, these theories being advanced by MacLeay (1830), Newport (1839), Hagen (1889), and Patten (1890), the two latter authors cited by Martin (1916), Lowne (1890), Comstock and Kochi (1902), Crampton (1909), Snodgrass (1909a), and others. Audouin, cited in MacLeay (1830), recognized three segments and his interpretation then is essentially the one accepted today. The sclerites which he named prescutum, scutum, scutellum, and postscutellum, he regarded as subdivisions of a single segment. MacLeay (1830) referred to the thoracic segments as being the second, third, and fourth body segments, the head being considered a single segment. Newport (1839) also based his studies on the work of Audouin and called the prothorax, mesothorax, and metathorax, the second, third, and fourth body segments, each being composed of four subsegments or annuli represented in the dorsum by the prescutum, scutum, scutellum, and postscutellum. These he believed were partially fused in the pleural region and completely so in the sternal region. Crampton (1909) and Martin (1916) criticized both MacLeay and Newport for their theory but it is possible that their interpretation of this work is in error. MacLeay and Newport each designated clearly a definite prothorax, mesothorax, and metathorax and may have been using the term "subsegment" much in the way "sclerite" is used today to denote only a sclerotized area of the dorsum. As an example, after describing the four pieces of the mesothorax as praescutum, scutum, scutellum, and postscutellum, MacLeay stated "The above four pieces when united form the tergum of the mesothorax".

To support the view that the terms prescutum, scutum, scutellum, and postscutellum are incorrect when applied to larvae, it may be as well to review briefly the development of the thoracic tergum. Again there is confusion because of the different terminology used for various areas of a segment. Snodgrass (1931, 1935) considered the dorsal region of a segment as the dorsum, the ventral region as the venter, and the lateral region lying between the dorsum and the venter as the pleural area. A major sclerotized plate of the dorsum was named the tergum, the corresponding plate of the venter was the sternum, and a single plate or group of plates in the pleural region was the pleuron. Component elements of these major areas were designated as tergites, sternites, and pleurites respectively. This nomenclature has not been used by all research workers; for instance, Crampton (1914) applied the terms dorsum and venter to the entire upper and lower surfaces of the insect body respectively. The entire dorsal region of each segment was called the tergum, the ventral region, the sternum, while the component sclerotized plates of these regions were referred to as tergites and sternites respectively. The entire lateral region of the body was called the latus, while the lateral region of a distinct segment was the pleuron. The terminology advocated by Snodgrass will be used in this paper.

There is a system of primary segmentation in the bodies of many arthropods, including many holometabolous larvae, where the segments are separated by circular constrictions forming internal folds to which are attached the longitudinal muscles. When sclerotization of parts of segments took place, usually the internal fold bearing the muscle attachment, a small anterior sclerite, and a more extensive region posterior to the antecostal suture became

sclerotized leaving the posterior portion of the dorsum membranous. The internal ridge is the antecosta, generally marked outwardly by the antecostal suture, and the sclerotized transverse area preceding the antecostal suture, which morphologically is a part of the preceding segment, is the acrotergite. The definitive intersegmental conjunctiva is now the membranous area behind the large tergal plate, resulting in a condition of secondary segmentation. In the thorax, the generalized structure typical of secondary segmentation is retained in the Apterygota, and in nymphal and many larval Pterygota. The prothoracic tergum and sternum always lack antecostal and precostal elements which apparently have been lost by membranization in the neck or posterior regions of the head. The external surface of the prothoracic tergum may be marked with sutures having corresponding ridges on the inner side. Crampton (1918) and DuPorte (1919) have shown that these sulci, in the pronotum of *Dis-sosteira carolina* and *Rhomalea microptera* respectively, are integumental folds formed by mechanical stress and do not represent the prescutum, scutum, scutellum, and postscutellum as was formerly assumed.

It is in the mesothorax and metathorax that specific modifications have taken place to accommodate these areas to the development of and action of the wings. The structural modifications have been outlined by Snodgrass (1927, 1935). The increased development of the longitudinal muscles of the wing-bearing segments necessitated the development of plate-like apodemes from the antecostae of the mesotergum, metatergum, and first abdominal tergum which are known as the first, second, and third phragmata. Since the wing movements are brought about by the curvature of the terga in the pterothorax, the terga of the two segments had to be modified to respond as a unit to the pull of the flight muscles, by elimination of the intersegmental membrane. In the majority of winged insects, this has been effected in the following manner. The acrotergite of the mesotergum retains its usual form of a narrow flange whereas the acrotergite of the metatergum and of the first abdominal segment are enlarged and extend forward to the posterior margin of the tergum preceding. The expanded acrotergites become the postnotal plates of the mesothorax and metathorax. In many of the higher insects, the phragmata may become separated from the original tergum by secondarily developed lines of membranization and become more closely associated with either the preceding or the following segmental plate. It is possible, therefore, for the segment bearing the major flight wings to have both anterior and posterior phragmata. The postnotum, as designated by Snodgrass, is equivalent to part of the postscutellum suggested by Audouin (Snodgrass, 1909b), and this term has been used by Crampton (1914) and Martin (1916). The same sclerite has also been referred to as the pseudonotum by Snodgrass (1907).

To meet the strains imposed upon them by the wings, the terga of the wing-bearing segments have been strengthened by the development of various ridges on the inner surfaces through inflections of the integument. It is these sutures which divide the terga into the sclerites taken by earlier workers to represent various combinations of subsegments. According to Snodgrass (1935), these sclerites have no morphological counterparts in the terga of other segments. A prescutal suture with a corresponding internal ridge cuts off a narrow sclerite, the prescutum, immediately behind the antecostal suture. This sclerite may be variable in shape, and may be difficult to distinguish from the sclerite behind in cases where the prescutal suture is weakly defined or absent. The scutum, lying behind the prescutum, is usually the largest sclerite and bears on its margins the anterior and posterior notal wing pro-

cesses. It is separated from the scutellum by the scuto-scutellar suture, which is in the general form of an inverted "V". The scutellum may send a median tongue or shallow groove forward, dividing the scutum into two halves. Laterally, the posterior margins of the scutellum are prolonged into the axillary cords of the wings. The foregoing basic plan of the dorsum of a wing-bearing segment is, of course, subject to numerous modifications by movement of existing sutures and development of others.

In soft-bodied holometabolous larvae, the abdominal segmentation is for the most part primary in the sense that the longitudinal muscles remain attached to the original intersegmental lines, although there is a tendency for some of these muscles to become attached to other points of the integument (Snodgrass, 1935). According to Snodgrass, a typical abdominal tergum has the sclerotization in the form characteristic of a secondary segmental plate. Anteriorly there is a marginal or sub-marginal ridge, the antecosta, to which the principal longitudinal muscles have their attachments. Generally, the antecostal suture is faintly marked and the acrotergite may vary from a scarcely perceptible rim to a wide flange. In certain cases, the antecosta and the acrotergite are lost, the muscles becoming attached to the anterior edge of the tergum. Snodgrass also stated that in many insects, particularly in the larval forms, the dorsal sclerotization of the abdomen may be broken up into groups of segmental tergites. These tergites are identified by position as mediotergites or laterotergites, and the mediotergites may be subdivided again. In the larvae of some insects, particularly Scolytidae, sclerotization is almost entirely absent, and, therefore, the usual tergites are not defined. A similar situation is evident with respect to the pleural and sternal areas, with the result that both the thorax and abdomen are devoid of sclerotized plates typical of many larval forms.

From the foregoing review of the specialized development of sclerites defined as prescutum, scutum, scutellum, and postscutellum, these terms should not be applied to folds in the integument of soft-bodied larvae where such folds are in response to the pull of segmental muscles, and are not related to the development or function of wings. Parkin (1933), studying the larvae of anobiid beetles, recognized that the folds of the body wall could not be homologized with divisions of the segmental sclerites of adult insects, and accordingly devised a special nomenclature. Using his system, a complete thoracic segment consisted of seven folds, a prenotal, postnotal, two hypopleurals, two pedals, and a sternal. Anderson (1947) also departed from the use of terms restricted to adult structure in describing the folds of the body of weevil larvae although he still retained the sternellum in referring to a fold of the venter of the abdominal segments.

In the scolytid larvae studied, the dorsum of the prothorax is undivided and is referred to as the prodorsum. The dorsum of the mesothorax and metathorax is divided transversely by a groove into a small median fold, elliptical in shape, followed by a transverse fold extending the full width of the segment (Fig. 1). The anterior and posterior folds are designated as I and II respectively. The dorsum of each of the first eight abdominal segments is made up of folds I, II, and III (Fig. 2). The delimitation of the folds on segment 8 is very indistinct and can only be seen under optimum lighting conditions. The dorsum of the ninth abdominal segment is undivided, requiring no further designation, and the tenth segment is represented by the anal folds. Immediately above the dorsopleural groove on segments 1 to 8 of the abdomen, and on the metathorax, there is a fold indistinctly delimited by a groove proceeding anteriorly, ventral to the spiracle. These are referred to as dorso-

pleural lobes. The grooves marking these folds are missing on the first two thoracic segments; however, the areas can be identified by the presence of corresponding setae. Using this simplified system, there is no tendency to become confused with the specialized terms perscutum, scutum, scutellum, and postscutellum which are restricted to the thoracic sclerites of adult insects. The numbering sequence also indicates the relative positions of the different folds.

As in the discussion of the head capsule, only the setae on one side of the body segments, or one-half of the total number of setae, will be listed. Setae on the dorsal folds of the mesothorax, metathorax, and abdominal segments 1 to 8, are numbered laterally from the midline.

A lightly sclerotized oval area lateral to the midline of the prodorsum bears five setae, and an additional six setae are located between this sclerite and the prothoracic spiracle making a total of eleven (Figs. 1, 2). The mesothorax and metathorax have the same setal pattern. Fold I has one seta near the midline; fold II has seven setae in a transverse row (Figs. 1, 2). Seta 5 is separated from the remainder by an indistinct crease in the integument. The sixth and seventh setae are called alar setae and are on smooth areas created in the integument by the absence of spicules.

The typical arrangement of the setae on the dorsum of abdominal segments 1 to 8 is shown in Figs. 1 and 2. Fold I has a single seta near the midline, fold II has no setae, and fold III has five setae arranged in a transverse row. Number 1 is separated from the remainder by a distance greater than that separating any two of the others. Setae 1, 3, and 5 are longer than 2 and 4. A pair of setae is located dorsal to the spiracle and these are called spiracular setae; the anterior seta is more dorsal than the posterior one and is usually the smaller of the pair. The dorsum of the ninth segment is not divided into folds and bears three long setae and three setae less than one-half as long, in an irregular transverse row (Figs. 1 and 4). The tenth segment, represented by the anal folds, bears a pair of minute setae on the fold lateral to the anal opening (Fig. 4). These are not always evident as they may become slightly infolded around the anus.

Pleuron: Hopkins (1909) described an irregular groove or suture dividing the pleuron of each segment of the larva of *Dendroctonus valens* into an upper lobe, the epipleurum, and a ventral lobe, the hypopleurum, which, in the thorax, are said to represent the epimerum and episternum respectively. Schedl (1931), in the study of the morphology of the larva of *Gnathotrichus materiarius*, adopted Hopkins' terminology but restricted the term pleuron to an area above the longitudinal fold or pleural fold of Hopkins. This area is again divided by another longitudinal groove into a dorsal part, bearing the spiracles in segments 1 to 8, which Schedl called epipleurite, and a ventral part, the hypopleurite, but Hopkins called this latter lobe the epipleurite. The lobe ventral to the pleural fold which Hopkins called the hypopleurite, Schedl refers to as the sternellar area. The terminology given by Hopkins was also adopted by Kaston (1936) in his study of *Hylurgopinus rufipes* but he considered that the groove referred to as the pleural groove or suture is undoubtedly the dorsopleural fold as outlined by Snodgrass (1931, 1935). The lobe above the fold Kaston called by analogy the laterotergal, and that ventral to the fold, the laterosternal, although Snodgrass (1931) called the latter the pleuron.

In this study of scolytid larvae, the folds lying between the dorsopleural and pleuroventral grooves are called the pleuron. In abdominal segments 1 to 8 there is a distinct groove or infolding separating a dorsal and ventral lobe, which together comprise the pleuron (Fig. 2). This groove is not as distinct in the

thoracic segments or in the ninth abdominal segment. A dorsopleural line passing directly ventral to the spiracles in segments 1 to 8 of the abdomen separates the dorsum of the insect from the dorsopleural lobe, and a second line, the pleuro-ventral, separates the ventropleural lobe from the sternum. These lines are not as distinct in the thoracic and ninth abdominal segments, but the position of the areas involved can be determined from corresponding setae. The above interpretation of the pleural region appears to be in accordance with the position of the muscles of the body wall. Tergopleural and sternopleural oblique muscles are inserted on the pleural groove. Also, there are intrapleural muscles stretching from the dorsopleural and pleuroventral lines to the pleural groove.

A pair of setae lateral to the pedal area of the prothorax and borne on a small area of integument clear of spicules, indicates the position of the ventropleural lobe of the pleuron with the dorsopleural lobe absent. The area of both dorsopleural and ventropleural lobes is indicated in the mesothorax and metathorax by the presence of a single seta on each lobe (Fig. 2). The dorsal and ventral lobes of the pleuron of abdominal segments 1 to 8 are distinctly delimited by integumental creases, and each fold bears a pair of setae on small areas of smooth integument (Fig. 2). The pleural region of the ninth abdominal segment consists of a single fold bearing a single pair of setae, and the pleural region of the tenth segment cannot be distinguished as such.

Sternum: As in the case of the dorsum, terms have been used to describe the folds in the sternum which are more appropriately restricted to the anatomy of adult insects, or at least to larvae which have a sclerotized thorax and abdomen. Audouin (cited in MacLeay, 1830) considered the lateral and ventral areas of the thoracic segments as the pectus. According to MacLeay, if the sternum of each thoracic segment was at its maximum of development, it, like the tergum, would consist of four pieces, and these he named praesternum, sternum, sternellum, and poststernum. Newport (1839) adopted MacLeay's terminology, although he could not find a fourth subdivision. Crampton (1909) would not use the terminology given by MacLeay since it inferred a relationship with the tergum, that is, that each segment originally was composed of four annuli, and he substituted the terms presternum, basisternum, furcisternum, postfurcal sclerite, and spinasternum. Böving (1929a) divided the sternum into eusternal and sternellar areas. Roberts (1926) called the anterior and posterior areas of the sternum of the thoracic and first eight abdominal segments of some weevil larvae, sternal and sternellar folds respectively. Anderson (1947) also divided the sternum of weevil larvae into an anterior eusternal and posterior sternellar fold. Hopkins (1909) in his description of the larva of *Dendroctonus valens* designated the divisions of the sternum as sternal, sternellar, and poststernellar. Schedl (1931) and Kaston (1936), both working with bark beetle larvae, used a similar division of the ventral folds of both thorax and abdomen.

In soft-bodied scolytid larvae, there are no individual sclerites which can be designated as true sternites such as occur in some holometabolous larvae. Therefore, I do not think we are justified in giving to the integumental folds, which occur as a result of muscular tension, names such as presternum, sternellum, and poststernellum. DuPorte (1950) outlined his theory of the development of the thoracic sternum as follows: The definitive sternum is regarded as a composite structure formed by the union of two coxosternites with ventrosternites lying between the subcoxae. The latter may consist of a narrow transverse plate, the presternite, at the anterior edge of the segment, a larger mediosternite lying between the subcoxae, and a small intersegmental

plate, the spinasternite, bearing an internal process, the spina. This latter sclerite is found only between the first and second, and second and third segments. The composite plate formed by the union of the two coxosternites with the mediosternite is the eusternum. The sternal apophyseal pits lie in the laterosternal sulci and a strengthening ridge, the sternacosta, develops internally between the apophyses, being marked externally by the sternacostal sulcus which divides the mediosternite into an anterior and a posterior section. This sulcus frequently continues across the coxosternites dividing them into anterior and posterior parts also. Since the laterosternal sulci usually disappear, the definitive sternum then consists of an anterior plate, the basisternite, and a posterior plate, the furcasternite. When the spinasternite unites with the furcasternite anterior to it, the resulting sclerite is the sternellum. It can be seen, therefore, that the sternum appears to have developed from existing sclerites, and, accordingly, the integumental folds in the ventral region of soft-bodied larvae should not be construed as representing specific sclerites.

The sternal area of each thoracic segment and segments 1 to 7 of the abdomen is divided into four areas by shallow grooves. Anteriorly, there is a median area or mediosternal fold that is roughly triangular in shape on the prothorax and more broadly U-shaped on succeeding segments. The posterior limit of this fold juts into a narrow transverse fold at the posterior end of the prothoracic and mesothoracic segments and abdominal segments 1 to 7. This transverse fold is missing from the eighth abdominal sternum, and the sternum of the ninth segment is undivided. On each segment up to and including the eighth abdominal, there is a laterosternal fold on either side of the median fold. A small, sclerotized circular area bearing four setae is located on each lateral lobe of the three thoracic segments.

The number and location of the setae on the sternum is indicated in Figs. 2 and 3 and, as in the description of the dorsum, the number of setae given represents those present on one-half of the body only. There is a single seta present on one side of the midline of the mediosternal fold in each thoracic segment, and a pair of setae in the corresponding location on abdominal segments 1 to 8. Each thoracic segment has a slightly sclerotized pedal lobe bearing four setae, and three setae on the laterosternal fold. The laterosternal fold of each abdominal segment 1 to 8 has a single seta. The sternum of the ninth segment is a single fold and bears two setae.

COMPARATIVE ANATOMY

A comparison of the larval anatomy of the 30 species examined is presented in this section; the head capsule, mouthparts, thorax, and abdomen being discussed separately. Characters appearing to link one or more genera, or conversely of use in delimiting genera and separating species within genera, are indicated, particularly those that merit further consideration for taxonomic and phylogenetic purposes when additional species become available. A practical adaptation of the information derived from the present study is demonstrated by the preparation of a key for the separation of 15 genera represented by the 30 species.

Head Capsule

The head capsules of nearly all species studied were free as opposed to retracted; that is, the entire or nearly the entire head capsule was visible with only a slight retraction into the folds of the prothorax. The head capsules of *Phloeosinus canadensis*, *Trypodendron lineatum*, and *Scolytus piceae* are exceptions to this usual condition, being partially retracted into the prothoracic

dorsum. In these species, dorsal epicranial setae 1 and 2 and the posterior epicranial setae are either located more anteriorly than in other species, as in *P. canadensis* and *S. piceae* (Figs. 17 and 19), or are in the usual position but greatly reduced in length, as in *T. lineatum* (Fig. 18). Head capsules of representatives of the 15 genera studied are shown in Figs. 6 and 17 to 31. The general shape varies from those of the majority that are approximately as broad as long, with curving sides and narrowly or broadly rounded posterior margins, to those that are slightly longer than broad, with sub-parallel sides and rounded posterior margins. The latter, represented by *P. canadensis* and *S. piceae* (Figs. 17 and 19), appear much longer than wide, an illusion created by the sub-parallel sides, which is not borne out by actual measurements.

The shape of the frons is variable between genera, although always of the same general appearance. The posterior margin may vary from acute-angled, as in *Hylurgops pinifex* (Fig. 6) and *Pityogenes hopkinsi* (Fig. 25), to broad, as in *Gnathotrichus materiarius* (Fig. 31), or rounded, as in *Crypturgus atomus* (Fig. 28). The frons may be as broad as or broader than long. The midcranial suture is usually distinct, extending from the posterior end of the frons anteriorly approximately half the length of the frons. The surface of the frons may present features of value in identifying certain species. Larvae of *Ips pini* have a pair of small tubercles situated about midway of the length of the frons (Fig. 21). These are unique among those species studied. Mature larvae of *H. pinifex* have a median tubercle located at the anterior edge of the frons (Figs. 6 and 8) which is also unique. The surface of the frons of species of the genus *Dendroctonus* has transverse, rugose areas not found in other genera.

The antennae are small, consisting of a central, conical process located on a membranous, basal portion. This basal section bears a number of setae, usually minute, but in certain cases one or more of these may be longer than the remainder. In *Phloeosinus canadensis* and *Scolytus piceae* (Figs. 17 and 19), one seta, mesad of the antenna, extends beyond the tip of it.

With a few exceptions, the head capsules are amber or light brown with darker areas across the anterior part of the frons and around the mandibular articulatory processes. In *Scolytus piceae*, *Phloeosinus canadensis* and *Typodendron lineatum*, the head capsule pigmentation is almost entirely lacking, a feature which readily separates these three from the remainder of the species under consideration. The pattern created by non-pigmented areas of the head capsule of *Gnathotrichus materiarius* is also distinctive (Fig. 31). A pair of narrow, unpigmented bands, one on each side of the coronal suture and parallel to it, runs posteriorly from the proximal region of the frontal suture. A second pair extends from near the distal end of the frontal suture posterolaterally to the sides of the cranium. In the genus *Pityophthorus*, there is occasionally an indistinct area on either side of the coronal suture beginning at the frontal suture which has less pigment than the remainder of the cranium (Fig. 29).

The distribution of setae on the head capsules of species within the same genus conform to one pattern, although a few differences occur between genera as is apparent from Figs. 6 and 17-31. The distribution of setae and sensilla on the head capsules of the 15 genera studied are compared in Table I. Eight genera, listed at the bottom of the table, have the same number of setae and sensilla, and these common numbers are inserted in column one of the table opposite the names given to them. Minor differences in numbers of setae and sensilla occur in the remaining seven genera and these are noted

under respective generic headings. Blanks in the table indicate that the number of setae or sensilla found agrees with the number in column one. Minor variations in number and position of setae occasionally occur between specimens of one species, and the symmetry of the head capsule is upset at times by the absence of a seta or the presence of an additional one.

The number of setae found on the head capsule of *Gnathotrichus materiarius* differs from that reported by Schedl (1931) for the same species. A number of specimens of this species were examined and considerable variation was found in numbers of setae in the dorsal epicranial group lateral to the coronal suture, the number ranging from seven to eleven with eleven being most common. The number of setae on the frons parallel to the frontal suture varied by one, either five or six being present, with six most common. The most anterior seta of this group, mesad of the antenna, corresponding to the seta epistomalis of Schedl, was always present. The group of five setae lateral to the frontal suture, which have been included here with the dorsal epicranial setae, would represent the group of five called seta geno-mediana by Schedl.

TABLE I
Distribution of Setae and Sensilla on the Head Capsule

	Genera listed below*	<i>Orthotomicus</i> (1)	<i>Ips</i> (5)	<i>Phloeosinus</i> (1)	<i>Scolytus</i> (1)	<i>Gnathotrichus</i> (1)	<i>Conophthorus</i> (2)	<i>Pityophthorus</i> (6)
Dorsal epicranial setae.....	5					13-17		
Posterior " ".....	4	5	5	3	3	5	4-5	4-5
Lateral " ".....	2							
Ventral " ".....	2							
Frontal setae.....	5				6	6-7		
Clypeal ".....	2							
Dorsal epicranial sensilla.....	3							
Posterior " ".....	1							
Lateral " ".....	2					4		
Ventral " ".....	1							
Frontal sensilla.....	2							
Clypeal ".....	1							

*The following genera have the number of setae and sensilla listed in the first column of the table. The number of species examined in each genus is given in brackets after the generic name.

Crypturgus (1) *Polygraphus* (1) *Dendroctonus* (4) *Hylurgops* (1)
Trypodendron (1) *Pityogenes* (2) *Pityokteines* (1) *Dryocoetes* (2)

Similarly, the ventral and lateral epicranial setae correspond to Schedl's genolateralis, although the number four found disagrees with the six listed by Schedl. The five minute posterior epicranial setae found on all head capsules examined were not listed by Schedl. No sensilla were listed by Schedl nor are they shown in any of his figures. It is possible, however, that certain of these were included as small setae.

The shape of the clypeus usually is quite similar in all species with a broadly emarginate anterior margin and sides angular to broadly rounded (Figs. 8 and 55-68). The anterior margin in species of the genus *Pityophthorus* (Fig. 65) is more deeply emarginate than in other genera. The posterior edge of the labrum in most species is attenuated and is located below the anterior half of the clypeus. It is darkly pigmented and the shape of it, when seen through the clypeus, may lead one to think that the anterior margin of the clypeus is deeply

cleft when such is not the case. There is usually a darkly pigmented band across the base of the clypeus, an area which has been indicated on the drawings by dotted lines. The shape and extent of the area may vary from a narrow band following the contour of the frontoclypeal suture, as in *Phloeosinus canadensis*, *Scolytus piceae*, and *Dryocoetes americanus* (Figs. 61, 62, and 63 respectively), to a wide band with a sinuate anterior margin, as in *Dendroctonus rufipennis* or *Ips perturbatus* (Figs. 55 and 58 respectively). The clypeus of all species studied had two setae and one sensillum located near the base. In the genera *Dendroctonus* and *Pityokteines*, clypeal seta 2, the outer of the two, varies from minute to less than one-half the length of seta 1 (Figs. 55 and 57 respectively). In the figures of the clypeus of *D. valens* by Hopkins (1909), only a single seta is shown on either side of the clypeus and no mention is made of them in the text. In *D. simplex*, clypeal seta 2 is approximately one-half the length of seta 1. In *Crypturgus atomus* and *Phloeosinus canadensis* (Figs. 56 and 61 respectively) both setae are equal in length. In the remaining genera, clypeal seta 2 varies from one-half to slightly less than the length of number 1. Schedl (1931), in his study of *Gnathotrichus materiarius*, listed only one seta on each side of the clypeus, whereas all the specimens examined here had two, the outer seta being approximately one-half the length of the inner one.

Mouthparts

Labrum: The labrum usually is narrower than the clypeus, broader than long, sides parallel or sub-parallel. The anterior margin varies from almost straight, as in *Dendroctonus* (Fig. 55), to a slight, median protuberance on the anterior margin, as in *Pityokteines* (Fig. 57). The posterior region of the labrum is attenuated and extends below the anterior end of the clypeus, being visible dorsally through the clypeus as a more darkly pigmented area. This has been indicated by a dotted line in Figs. 8 and 55-68 which are representative of the fifteen genera studied. The labrum is mostly uniformly pigmented, with the exception of *Phloeosinus canadensis* and *Scolytus piceae* in which the labrum has an area at the posterior end, indicated by dotted lines in Figs. 61 and 62 respectively, more darkly pigmented than the remainder. The outline of the tormae is visible dorsally through the labrum and clypeus, and has been indicated by dotted lines in Figs. 8 and 55-68. The free ends of the tormae are separate, except in *Hylurgops pinifex* (Fig. 8), in which the posterior ends curve mesally and a weak line of fusion may occur, and in *Trypodendron lineatum* (Fig. 68), in which the posterior ends of the tormae were fused in all the specimens examined. With the exception of the labrum of *Gnathotrichus materiarius* (Fig. 67), which has a single pair of dorsal setae only, all other species have three pairs of dorsal setae, the median pair of which is longer than the other two. Most species have a median and a pair of lateral sensilla on the labrum, although these are frequently indistinct.

Epipharyngeal lining: The anterior margin of the labrum is reflexed and is continued into a semi-membranous lining of the labrum and clypeus extending into the oesophagus. This lining bears a number of setae, the number and arrangement of which are shown in Figs. 16 and 69-89. The reflexed anterior margin of the labrum bears two, three, or four anteromedian setae. The majority of the species have only two anteromedian setae, but three are present in the genera *Conophthorus* and *Pityophthorus* (Figs. 73 and 74 respectively), and four in the species of *Ips* studied (Figs. 81-85). In the latter, the inner two are large and stout, while the outer two are much smaller, slender, and frequently difficult to see. A group of three anterolateral setae is present on either side of the

median setae. The inner two anterolateral setae of each group are sometimes absent from specimens of *Trypodendron lineatum* (Fig. 80) and are usually inconspicuous when present.

The median epipharyngeal setae are usually in pairs located in median, longitudinal rows between the labral tormae. There is considerable variation in the number and arrangement of these setae. *Trypodendron lineatum* (Fig. 80) has none. Three pairs are present in the genera *Hylurgops*, *Crypturgus*, *Phloeosinus*, *Conophthorus*, *Pityophthorus*, *Dryocoetes*, *Polygraphus*, and *Dendroctonus* (Figs. 16, 69, 71, 73-78, and 86-89). In *Phloeosinus canadensis* (Fig. 71), the two anterior pairs are grouped around the anteromedian setae in a compact group of six setae. There are four pairs in *Scolytus piceae* (Fig. 70) with the two anterior pairs arranged in a crescentic formation posterior to the anteromedian setae. *Orthotomicus caelatus* (Fig. 72) has a row of eight pairs of median setae aligned closely from the anterior margin of the labrum to the posterior ends of the tormae. *Ips* is the only genus in which the number of median epipharyngeal setae varied between the species studied. *I. pini* and *I. borealis* (Figs. 81 and 84 respectively) have eight pairs of setae, whereas *I. calligraphus*, *I. perturbatus*, and *I. chagnoni* (Figs. 82, 83, and 85) each have eleven pairs. Only a limited number of specimens of *borealis*, *calligraphus*, and *chagnoni* were available for examination however, and a longer series might not support these figures. Considerable variation in the number and position of the median epipharyngeal setae occurred between specimens of *Gnathotrichus materiarius*. The arrangement shown in Fig. 79, with three anterior pairs of setae, two single sensilla in vertical alignment followed by two setae in vertical alignment, and finally two more sensilla, occurred most commonly. This arrangement does not agree with that found by Schedl (1931), who described an anterior pair of setae or apical papillae and a median row of sensilla. The surface of the epipharyngeal lining of all species studied, with the exception of *Crypturgus atomus* and *Trypodendron lineatum*, bears sensilla, either singly or in clusters, along with the median epipharyngeal setae.

Mandible: The use of mandibular characteristics for taxonomic purposes should be approached with caution, since the teeth wear and do not always present the same clearly defined characteristics found at the beginning of a stadium. The characteristics discussed here and shown in Figs. 91-105 are those found on mandibles from newly-moulted larvae. One species, *Scolytus piceae* (Fig. 93), has only two incisoral teeth; the remainder of the species studied have three incisoral teeth, and *Hylurgops pinifex* (Fig. 105) has a minute fourth tooth near the middle of the incisoral edge of the mandible. The genera in this latter group may be sub-divided into those in which the apical and sub-apical teeth are acute and the third tooth is emarginate, *Ips*, *Pityogenes*, *Dryocoetes*, *Dendroctonus*, *Orthotomicus*, and *Hylurgops* (Figs. 91, 92, 96, 103, 104, and 105), and those in which all three teeth are acute, *Crypturgus*, *Polygraphus*, *Trypodendron*, *Pityokteines*, *Phloeosinus*, *Gnathotrichus*, *Conophthorus*, and *Pityophthorus* (Figs. 94, 95, and 97-102). The dorsal surfaces of the mandibles of certain species are smooth, while in others they are rugose or bear transverse ridges. The distal half of the mandible of *Polygraphus rufipennis* is slightly less thick than the basal half, giving the effect of a ridge across the middle (Fig. 95). In *Pityokteines sparsus*, there is a transverse ridge across the centre of the dorsal surface (Fig. 98).

The mandibles of all species examined have two dorsal setae and three sensilla. A single sensillum is present on the inner dorsal surface, and two sensilla, usually close to each other, near the basal edge of the dorsal surface. The arrangement of the setae divides the fifteen genera into two classes. In the genera *Gnatho-*

trichus, *Conophthorus*, *Pityophthorus*, *Dendroctonus*, and *Hylurgops* (Figs. 100-103, and 105 respectively), the setae are in vertical alignment, whereas in the genera *Ips*, *Pityogenes*, *Scolytus*, *Crypturgus*, *Polygraphus*, *Dryocoetes*, *Trypodendron*, *Pityokteines*, *Phloeosinus*, and *Orthotomicus* (Figs. 91-99, and 104 respectively), they are close together and arranged more or less horizontally.

Maxilla: The maxillae of all the species studied resemble each other fairly closely and offer only a few characters suitable for separation of genera and species. The usual colour is a uniform amber or light brown, with the exception of *Phloeosinus canadensis* and *Scolytus piceae* in which a section of the ventral surface of the stipes is unpigmented. In *P. canadensis* (Fig. 44), the unpigmented area occupies nearly the entire length of the stipes, and has stipital seta 1 located at its anterior end and a sensillum near the posterior end. The unpigmented area in *S. piceae* (Fig. 45) is small and medially located with stipital seta 1 in it, but the sensillum is in the pigmented area of the stipes. The palpi are 2-segmented and similar in most respects in all species, with the exception of *Pityogenes*, *Conophthorus*, and some species of the genus *Pityophthorus*. In many specimens examined, these had an accessory process on the outer distal part of the first segment of the palpus, approximately equal in length to the second segment of the palpus (Figs. 46 and 51). The process occurred commonly on specimens of *Pityogenes hopkinsi*, *P. plagiatus*, and *Conophthorus resinosa*, and less frequently on specimens of *C. coniperda* and of the genus *Pityophthorus*.

The number of setae and sensilla present on the stipes, palpifer, lacinia, and palpus is similar in the species studied. Some variation in position of the stipital and palpiferal setae occurs between species, as examination of Figs. 46-54 will show. Stipital seta 1 is usually located in the proximal third of the stipes, but is found about the midpoint in *Scolytus piceae* and *Gnathotrichus materiarius*, (Figs. 45 and 53), and in the distal third in *Phloeosinus canadensis* and *Trypodendron lineatum* (Figs. 44 and 54). Palpiferal seta 1, the outermost of the two, may be located on the edge of, or in, the membranous area at the base of the palpus. The inner palpiferal seta, number 2, usually is located in the membranous area, but occasionally may be on the edge of the membrane in the sclerotized area as in *Dendroctonus piceaperda* (Fig. 41).

Labium: Variations in the shape of the premental sclerite, the position of the postlabial setae, and the number of segments in the palpi, are useful in the key to genera and may provide valuable clues to taxonomic and phylogenetic relationships. The fifteen general can be divided into three groups on the basis of the shape of the premental sclerite. In the first group, the proximal part of the sclerite is attenuated to form a distinct projection more or less uniform in width from the base of the three anterior arms. The genera *Hylurgops*, *Dendroctonus*, *Crypturgus*, *Polygraphus*, *Phloeosinus*, and *Scolytus* (Figs. 9, and 41-45 respectively) comprise this group. In the second large group, the proximal part of the premental sclerite posterior to the three anterior arms is more in the form of a triangle. In most of the genera of this group, *Ips*, *Dryocoetes*, *Conophthorus*, *Pityophthorus*, and *Gnathotrichus* (Figs. 49-53 respectively), the triangular shape is definite, whereas in the genera *Pityogenes*, *Orthotomicus*, and *Pityokteines*, (Figs. 46-48), it is intermediate between the two groups. The third type of premental sclerite is found in the genus *Trypodendron* only (Fig. 54). The sclerite has three anterior arms as in groups 1 and 2, but the proximal part is roughly rectangular in shape and occupies the greater part of the postlabial region.

In certain species in groups 1 and 2, there is a median band of darker pigment extending from the end of the posterior projection either part or all of the distance

toward the tip of the median anterior arm. This may lead to a false impression of the true shape of the sclerite since the areas lateral to the darker area are frequently indistinct.

The labial palpi are distinctly 2-segmented in all but the genera *Pityophthorus*, *Conophthorus*, and *Gnathotrichus* (Figs. 51-53 respectively), in which the proximal segment is indistinct.

The arrangement of the three postlabial setae can also be used to group certain of the genera although these groups do not always contain the same genera as when based on the shape of the premental sclerite.

The arrangement of the six genera assigned to group one on the basis of the shape of the premental sclerite is varied. In the genera *Hylurgops*, *Dendroctonus*, *Crypturgus*, and *Polygraphus* (Figs. 9, 41-43 respectively), setae 1, 2, and 3 are arranged in the form of a triangle with seta 2 lateral to 1 and 3. This arrangement is useful in separating larvae of *P. rufipennis* and *Dryocoetes affaber* that are frequently found together, since the postlabial seta of the latter species are arranged in a straight line running anteromesally, similar to that shown for *D. americanus* (Fig. 50). Postlabial setae 1, 2, and 3 in the genera *Phloeosinus* and *Scolytus* (Figs. 44 and 45) fall on a line running anterolaterally.

In the genera *Pityogenes*, *Orthotomicus*, *Pityokteines*, *Ips*, *Dryocoetes*, *Conophthorus*, *Pityophthorus*, and *Gnathotrichus* (Figs. 46-53), postlabial setae 1, 2, and 3 fall on a straight line running anteromesally, an arrangement the reverse of that in genera *Phloeosinus* and *Scolytus*.

The postlabial setae of *Trypodendron lineatum* (Fig. 54), which is by itself on the basis of the shape of the premental sclerite, are located so that lines drawn through the three setae on either side are more or less parallel. Seta 1 is located on the posterolateral areas of the premental sclerite, with setae 2 and 3 close to the base of the lateral anterior arms.

The number of setae found by Schedl (1931) on the labium of *Gnathotrichus materiarius* differs from that on specimens of the same species examined in this study. Schedl indicated two setae in the areas between the median and lateral anterior arms of the premental sclerite, the anterior one of the two being quite short, and a single sensillum near the base of the palpus. In the specimens examined here, the reverse was found, a single seta but two sensilla being located near the base of the palpus. It is possible that in the specimens Schedl examined, one of the sensilla had developed into a small seta, or was mistaken for a seta. On rare occasions an extra seta was found on a specimen in a position normally occupied by a sensillum. Where two sensilla were found at the base of the lateral anterior arm of the premental sclerite (Fig. 53), Schedl located one sensillum and one seta.

Postcephalic integument

The postcephalic integument of the scolytid larvae studied, with the exception of three of the four species of the genus *Dendroctonus*, offers few features useful in separating genera, or species within genera. The number and location of the integumental folds are shown for *Hylurgops pinifex* (Figs. 1, 2, and 3). The paired pronotal plates, that are amber and quite distinct in *H. pinifex* and in certain other genera such as *Dendroctonus*, *Ips*, *Dryocoetes*, and *Polygraphus*, are only slightly pigmented and consequently are indistinct in *Orthotomicus*, *Scolytus*, *Conophthorus*, *Pityophthorus*, *Pityogenes*, *Trypodendron*, *Gnathotrichus*, and are practically unpigmented in *Phloeosinus*, *Pityokteines*, and *Crypturgus*. However, in those genera in which the pigmentation is slight or lacking, the pronotal plates become apparent after the integument is stained, because they take on and retain a deeper colour than the surrounding tissue. *Dendroctonus*

valens has a small, sclerotized plate lateral to each of the pronotal plates discussed above (Fig. 90). The small, sclerotized plate on the prothoracic sternum varies from deeply pigmented and clearly visible in *Ips*, *Dryocoetes*, *Polygraphus*, and *Scolytus*, to lightly or unpigmented, and consequently indistinct, in the remaining genera.

The thorax and abdomen of mature larvae usually are nearly equal in diameter, with the exception of *Scolytus piceae*, where the thorax is distinctly larger than the abdominal segments which taper toward the posterior end. As the larvae mature and reach the last instar and prepupal stage, the developing wings and legs cause the thoracic region to become enlarged, in particular forcing the development of distinct bulges or pedal lobes on the three thoracic sterna. The larvae also decrease in length during the prepupal stage and become very white as feeding ceases and food is no longer visible in the alimentary canal. These changes assist in the selection of mature larvae, which are preferred for study.

The larvae of *Dendroctonus valens*, *D. rufipennis*, and *D. piceaperda* have distinctive integumental characteristics which separate them from the larvae of all other species studied. The same characters can be used for the separation of the four species of *Dendroctonus* available for the study.

The eighth and ninth abdominal segments of these species have strongly sclerotized dorsal plates, brown or dark amber. The dorsal plates of *valens* are fused into a single, large plate armed with seven relatively sharp projections (Fig. 38) in two transverse rows of three each, and a single, median projection dorsal to the anus. In *rufipennis* and *piceaperda*, there are single, dorsal plates on the eighth and ninth segments, and a faint trace of a plate on the seventh segment (Figs. 36 and 37). In *piceaperda*, the sclerotized plates are slightly rugose, whereas those of *rufipennis* have a pair of raised tubercles that are extremely rugose.

All three species have a sclerotized, amber tubercle dorsal to the prothoracic and abdominal spiracles (Figs. 32, 33, and 34). The spiracles are located in the ventral surface of the tubercles and are concealed when the larvae are viewed from above. The surface of the tubercle in *valens* is only slightly rugos, whereas that of the tubercles in *rufipennis* and *piceaperda* bear a number of definite asperities. The dorsopleural lobe of abdominal segments 1 to 8, those with spiracles, of *valens* and *rufipennis*, has a sclerotized, amber tubercle as shown in Figs. 32, and 33. In *valens*, the tubercles are large and extend beyond the spiracular tubercles when the larva is viewed from above. In *rufipennis*, the tubercles are smaller and are more in the form of a sclerotized area in the centre of the dorsopleural lobes. They do not extend beyond the spiracular tubercles. The dorsopleural lobes of *piceaperda* are not sclerotized, and are not protuberant (Fig. 34).

D. simplex, the fourth species examined in this genus, is readily separated from the others by the absence of sclerotized plates on abdominal segments 8 and 9, and of tubercles over the spiracles (Fig. 35).

The setal pattern differs in certain respects between genera but, with the exception of one species, *Dendroctonus rufipennis*, is the same within genera. Slight variations in number and position of setae between specimens of the same species may occur, and minor variations in the position of setae on corresponding lobes or folds of two halves of a specimen occasionally destroy the symmetry. The setal patterns of certain segments are similar and can be grouped as follows for comparative purposes. The mesothoracic and metathoracic patterns are alike but differ from that on the prothorax. The patterns on the first eight abdominal

segments are alike except in *Gnathotrichus materiarius*, where the number of setae on the eighth segment differs from that on 1 to 7. The ninth and tenth segments are considered separately. The arrangement of the setae on the body of *Hylurgops pinifex* is typical, and differences between the setal patterns of other genera and the typical one are in number, position, and relative conspicuousness.

To facilitate comparison of the number of setae found on larvae of different genera, Fig. 106 has been prepared. The left-hand column lists the name applied to groups of setae, or to lobes and folds of the body on which setae are located, divided into segments or groups of segments as previously discussed. The names of the genera examined are arranged at the top of the chart as column headings and, where more than one species in a genus was studied, the number of species is inserted in brackets. In a special column at the left of the generic columns, headed "Model No. of Setae", the number of setae most common to the larvae of the different genera has been inserted. Blanks in generic columns indicate that the number of setae found on the larvae examined agrees with the model number. Differences are noted by inserting in the respective square, the actual number of setae found. Examination of the chart shows that slight variations in numbers of setae present on different parts of the body occurred in 9 genera.

The structure of the spiracles may add additional evidence to support or refute a determination of a genus arrived at from other larval characters. Spiracles are located on the prothorax and first eight abdominal segments of scolytid larvae. They are of two types; circular as in Fig. 14, found in *Phloeosinus canadensis*, *Scolytus piceae*, *Trypodendron lineatum*, and *Gnathotrichus materiarius*, or a circular orifice with a pair of annulated air tubes lateral to the orifice (Fig. 13) found in the remainder of the genera. The prothoracic spiracle is invariably larger than those on the abdomen, and the first abdominal is usually, but not always, larger than those on segments 2 to 8. The length of the air tubes varies from approximately one-half to twice the width of the circular orifice. The usual position of the air tubes on the prothoracic spiracle is vertical, while those on abdominal spiracles are posterolateral, except in *Hylurgops*, *Dendroctonus*, and *Ips*, where they are obliquely vertical with the extremities pointing posteriorly.

Identification of Species Examined

The information presented in the preceding paragraphs has been drawn upon to demonstrate now an immediate use for detailed studies of larval anatomy. A key based on some of the larval characteristics described previously has been prepared with which it is possible to determine to the genus 30 species in the 15 genera examined. Although the small number of species examined limits the application of the key, definite evidence is presented that identification of larvae is practicable. Of the 15 genera available, 7, *Crypturgus*, *Gnathotrichus*, *Hylurgops*, *Orthotomicus*, *Phloeosinus*, *Pityokteines* and *Polygraphus*, are represented by only one species in Eastern Canada. The genus *Scolytus* has only one species breeding in coniferous trees in Eastern Canada. Therefore, in these instances, it is possible to obtain a specific identification of the specimens. The remaining 7 genera are represented by more than one species. Of these genera, all species represented in Eastern Canada of *Dendroctonus*, *Dryocoetes*, *Pityogenes*, and *Conophthorus* were available for study; however, it was only in the genus *Dendroctonus* that it was possible to separate the species. In the genus *Ips*, of which five species were available, only *Ips pini* could be separated from the remainder. With the exception of these two particular cases, the specimens can be identified to genus only. The key has been prepared using mature and prepupal larvae for the most part since, at the time the keys are usually required,

it is these stages which are most likely to be found. To test whether the characteristics of mature larvae are also present in younger larvae, two species were checked. Larvae of *Ips pini* of varying sizes ranging from very minute, probably first instar, to prepupae, were examined and no anatomical differences were noted. This species can be identified by the presence of a pair of tubercles on the frons, and these were present on the smallest sized larvae examined although they were not as apparent as on mature larvae. Larvae of *Hylurgops pinifex* were also examined, and the setal pattern on the head, mouth parts, and the body was the same on all sizes of larvae checked. The only anatomical difference noted was the absence of the median tubercle from the frons on some of the very small larvae. This tubercle is usually quite evident in mature larvae.

Key to Genera and Species

1. Proximal part of the premental sclerite of the labium triangular (Figs. 52, 53) or a distinct projection of the main body of the sclerite (Figs. 45, 46) 2
 - Proximal part of the premental sclerite broadly rectangular, lightly pigmented (Fig. 54) *Trypodendron lineatum*
2. Postlabial setae in a triangular arrangement, setae of middle pair farthest apart (Figs. 9, 41) 3
 - Postlabial setae not arranged as above 6
3. Postlabial seta 2 closer to 3 than to 1, large species (Figs. 9, 41) 4
 - Postlabial setae equally spaced or 2 only slightly closer to 3 than to 1, small species (Figs. 42, 43) 5
4. A single tubercle located on the median anterior margin of the frons in mature specimens (Fig. 6) *Hylurgops pinifex*
 - No tubercles located on the frons *Dendroctonus*
5. Posterior margin of the frons rounded, frontal setae 1 and 2 close together and located in the posterior area; frontal sutures indistinct; very small species (Fig. 28) *Crypturgus atomus*
 - Posterior margin of the frons acute, frontal seta 2 located one-half the distance between 1 and 4; frontal sutures distinct; larger species (Fig. 27) *Polygraphus rufipennis*
6. Postlabial setae arranged in a straight or slightly crescentic line proceeding from seta 1 anterolaterally, the distance between setae 1 less than that separating either of the other two pairs of setae (Figs. 44 and 45) 7
 - Postlabial setae arranged in a straight or slightly crescentic line proceeding from seta 1 anteromedially, the distance between setae 1 greater than that separating either of the other two pairs of setae (Figs. 46 and 47) 8
7. A non-pigmented area occupying at least two thirds of the ventral surface of the maxillary stipes; the lateral anterior arms of the premental sclerite of the labium join the base of this sclerite obliquely (Fig. 44) *Pbloeosinus canadensis*
 - The non-pigmented area occupying less than one-third of the ventral surface of the maxillary stipes; the lateral anterior arms of the premental sclerite of the labium join the base of this sclerite at right angles (Fig. 45) *Scolytus piceae*
8. Dorsal epicranial setae of the head capsule in excess of 5 (Fig. 31) *Gnatbotrichus materiarius*
 - Dorsal epicranial setae of the head capsule 5 or fewer in number 9
9. Labial palpus apparently 1-segmented (Figs. 51, 52) 10
 - Labial palpus distinctly 2-segmented 11
10. Anterior margin of the clypeus usually deeply emarginate; darkly pigmented area at the base of the clypeus narrow; torma slender (Fig. 65); usually three laterosternal setae on thoracic segments *Pityophthorus*
 - Anterior margin of the clypeus broadly emarginate; darkly pigmented band at base of clypeus narrow in the middle increasing to almost a third of the depth of the clypeus on either side; torma stout (Fig. 66); usually four laterosternal setae on the thoracic segments; larger species *Conophthorus*
11. Three pairs of median epipharyngeal setae (Figs. 75, 76, 77) 12
 - More than three pairs of median epipharyngeal setae (Figs. 72, 81) 14
12. Clypeal seta 2 minute, much shorter than seta 1 (Fig. 57); a narrow non-pigmented strip beginning at the frontal suture extends parallel to and on either side of the coronal suture (Fig. 24) *Pityokteines sparsus*
 - Clypeal seta 2 approximately one-half the length of seta 1 (Figs. 60, 63); dorsal epicranial area evenly pigmented 13

13. Posterior projection of the premental sclerite of the labium distinct from the body of the sclerite for at least one-third of the total length of the sclerite (Fig. 46).....*Pityogenes*
Posterior area of the premental sclerite triangular in shape (Fig. 50).....*Dryocoetes*
14. Anteromedian setae of the labium four in number, the outer pair shorter and more slender than the inner pair (Figs. 81 to 85).....*Ips*
Anteromedian setae of the labium two in number (Fig. 72).....*Orthotomicus caelatus*

DISCUSSION

In the preceding account of the comparative larval anatomy of a number of species of bark beetles, certain characteristics of various parts of the body appeared to link two or more genera. A few of these characteristics now are grouped to indicate possible affinities between genera more readily than they can be from the overall comparative anatomy section.

The shape of the premental sclerite of the labium and the arrangement of the postlabial setae described at length in the earlier part of the paper apparently permit the most clearly defined grouping of genera. *Ips*, *Orthotomicus*, *Dryocoetes*, *Gnathotrichus*, *Pityogenes*, *Pityokteines*, *Conophthorus*, and *Pityophthorus*, subfamily Ipinae, have the postlabial setae 1 to 3 arranged in a straight line running anteromesally, with the greatest distance between setae 1. The arrangement of these setae in *Trypodendron lineatum*, the only other species studied of the subfamily Ipinae, is intermediate between that typical of genera in Ipinae and that in genera in the subfamily Hylesininae, the lines drawn through postlabial setae 1-3 being more or less parallel. This species, however, belongs by itself on the basis of the distinctly shaped larval premental sclerite.

The apparently 1-segmented labial palpi of *Pityophthorus*, *Conophthorus*, and *Gnathotrichus* indicate a possible relationship between these three. While *Gnathotrichus* has a pattern in the head capsule made by lack of pigment in certain areas, which is not exactly duplicated in other genera, there is a pigmentation pattern on a reduced scale in *Conophthorus* and occasionally in *Pityophthorus*. An accessory process on the basal segment of the maxillary palpus suggests another bond between *Pityophthorus* and *Conophthorus*, and the presence of the same process in some specimens of *Pityogenes* indicates a possible link between these genera. Additional evidence of a close link between *Conophthorus* and *Pityophthorus* is the presence of three anteromedian setae of the epipharyngeal lining in place of the two or four found in other genera. Opposed to the characters possibly linking these genera, the distinctive setal pattern on the head of *Gnathotrichus* sets it apart from the other two.

One of the most distinctive features of the species of *Ips* is the comparatively large number of median epipharyngeal setae. Most other genera have three or four pairs but all specimens of *Ips* species have more than five pairs. A strong factor in linking the genus *Orthotomicus* to *Ips* is the presence of five or more pairs of median epipharyngeal setae. The two mandibular setae in these genera are similarly arranged in a semi-horizontal alignment as opposed to definitely vertical or horizontal in position.

Scolytus piceae, which in the adult stage quite clearly features the characteristics of the subfamily Scolytinae, appears to have one larval characteristic, a bilobed mandible, that is unique among those species studied. This species and *Phloeosinus canadensis*, which are in different subfamilies in adult classifications, display a number of interesting points of similarity. An unpigmented area on the ventral side of the stipes is peculiar to these species. The pigmented patterns on the labrum are more or less similar and differ from those found in other species. Pigmentation is almost lacking in the head capsules, and the sides of the head capsules are straight, rather than curved as is the case in most other species studied.

Dorsal and posterior epicranial setae are located more anteriorly than in other species, a factor possibly correlated with the retraction of the head into the prothorax. Also there are three posterior epicranial setae in place of the four or five found in most other genera. The spiracles are circular in both species. In each species, one of the setae at the base of the antenna exceeds the length of the antennal article.

Nearly all genera have sensilla as well as setae on the epipharyngeal lining. In this respect, *Dendroctonus*, *Polygraphus*, and *Hylurgops* have clusters of three sensilla not present in other genera, which may be indicative of a relationship between the three. The arrangement of the postlabial setae and the shape of the premental sclerite in these three genera are almost identical, another indication of a possible affinity between the three.

Successful achievement of the minimum objective of separating larvae of different genera and species necessarily points toward application of the same characteristics or combinations of them to indicate relationships within the family Scolytidae and in the order Coleoptera as a whole. In theory, grouping of species into genera and genera into subfamilies on the basis of either adult or larval anatomy should result in a similar organization. If not, it would indicate that the interpretation of the evidence has been incorrect, the evidence from one or other of the forms is incomplete, or that a satisfactory system of classification can only be founded on a consideration of adult and larval characteristics together rather than independently. The following quotation from a paper by Swaine and Hopping (1928) on the tribe Lepturini of the family Cerambycidae conveys much the same thought. These authors had arranged the genera of this tribe according to a study of adult characters and Dr. Craighead prepared a list indicating the generic grouping suggested by larval characters alone. It differed from their arrangement and evoked the comments quoted:

"It is perhaps hardly to be expected that the grouping made from the larval characters will, in all cases, conform to that made from adult characters. It appears reasonable to suppose that the similar habitat of the larvae, mostly wood borers, may have checked a tendency toward divergence in characters that may have found freer expression in the adults; and, on the other hand, that the similar habitat may have resulted in convergence through the reduction of larval characters or the evolution of similar characters in groups at one time definitely separated."

Results of this study, while admittedly based on a limited number of species and genera, indicate that consideration of both larval and adult characters must be given serious thought. Grouping of genera into subfamilies on the basis of larval anatomy appears difficult at present, and it is apparent that the conventional classification of the family Scolytidae is not as clearly defined as one would expect from a review of the literature based on adult anatomy alone. These observations, however, may instigate some searching reviews of existing classifications based on adults alone, and promote the development of a revised system compatible with both adult and larval characteristics.

Continuation of the study of larval anatomy beyond the introductory phases described in this paper will, it is hoped, bring forth a solution to the problem of separating larvae of the families Scolytidae and Curculionidae. The literature review conducted preparatory to undertaking this study, and during the course of it, revealed that the immature stages had been used more extensively for separation of genera and species in Curculionidae than in Scolytidae. Important contributions have been made by Roberts (1926), Böving (1929a), VanEmden (1938), and Anderson (1941, 1947, 1948a, 1948b, 1952). In many of the pub-

lished keys to beetle larvae, the two families appear together since the authors either claim directly or infer that the larval forms are inseparable. Such is the case in the publications of Roberts (1930), Böving and Craighead (1931), Gardner (1934), Chu (1949), and Peterson (1951). Crowson (1955) in his recent work on a natural classification of the Coleoptera has dropped Scolytidae entirely from his system of classification and included the species in Curculionidae. One of his reasons for doing this has been that he was unable to characterize satisfactorily the Scolytidae in the adult state. However, it has been shown by certain authors that scolytid and weevil larvae can be separated in specific instances. Wallace and Beard (1942) described a method for separating the larvae of two species of bark beetles, *Scolytus multistriatus* Marsh. and *Hylurgopinus rufipes* Eich., from two species of weevils, *Magdalis armicollis* Say and *M. barbata* Say, which frequently occurred together in the bark of elm trees. During the course of the research being reported on here, it was possible to separate larvae of three weevils, *Pissodes* probably *approximatus* Hopk., in white pine, *Pissodes* sp. in jack pine, and *Pissodes affinis* Rand. in white and black spruce, from the larvae of bark beetles found in association with them. Distinct, pigmented ocellar spots lateral to the antennae (Fig. 39) separate these larvae from the scolytid larvae, which do not have ocellar spots. Also, abdominal segments 2-7 of the weevil larvae have four dorsal folds in the integument (Fig. 40), which distinguishes them from scolytid larvae, which have only three. It appears contradictory that within the two families Scolytidae and Curculionidae, as presently constituted, larvae can be separated into genera and, in some cases, into species, yet, other than in a few isolated instances, no general characteristics have been found for separating these larvae at the family level.

ACKNOWLEDGMENTS

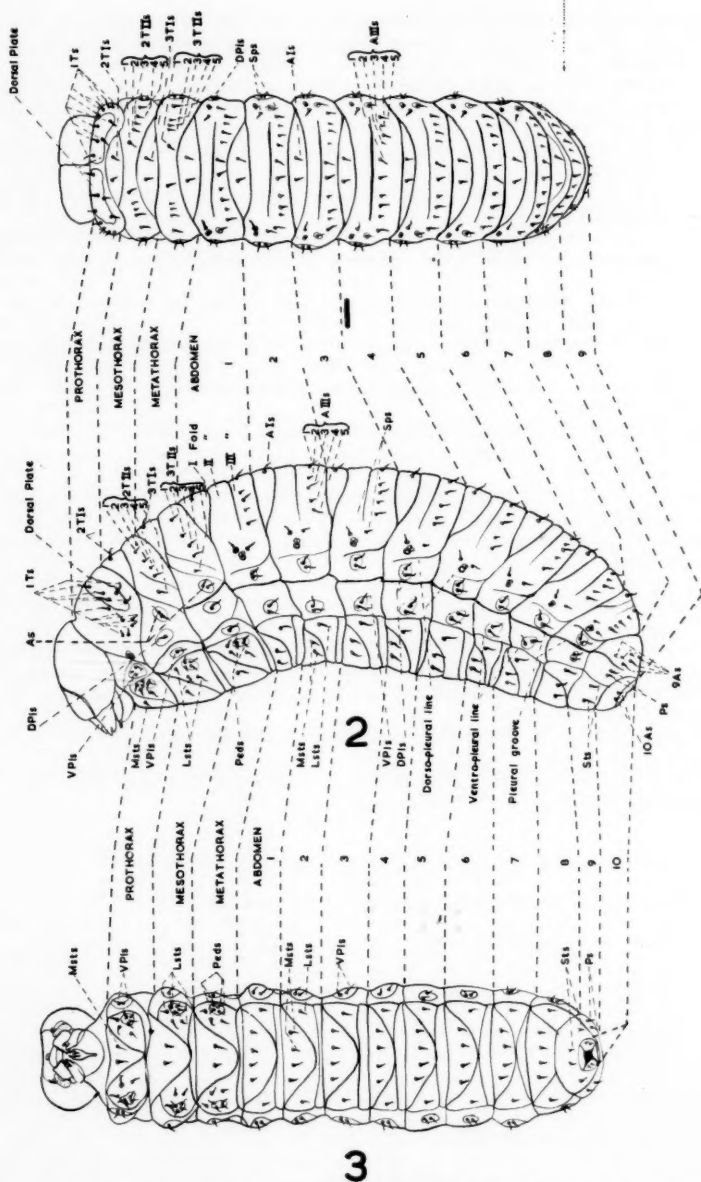
I am indebted to R. M. Belyea, S. G. Smith, and J. M. Cameron, Forest Insect Laboratory, Sault Ste. Marie, for a critical appraisal of the manuscript and many helpful suggestions. E. M. DuPorte, Professor of Entomology, Macdonald College, gave valuable assistance in the preparation of the original manuscript. S. L. Wood, Entomology Division, Science Service, Department of Agriculture, reviewed the points dealing particularly with phylogeny. The assistance of the following collectors and institutions in providing material is gratefully acknowledged. N. R. Brown, Professor of Entomology, University of New Brunswick; A. T. Drooz, United States Department of Agriculture, Forest Service, Division of Forest Insect Research, St. Paul, Minnesota; L. A. Lyons, Forest Insect Laboratory, Sault Ste. Marie; and the United States National Museum, Smithsonian Institution, Washington, D.C.

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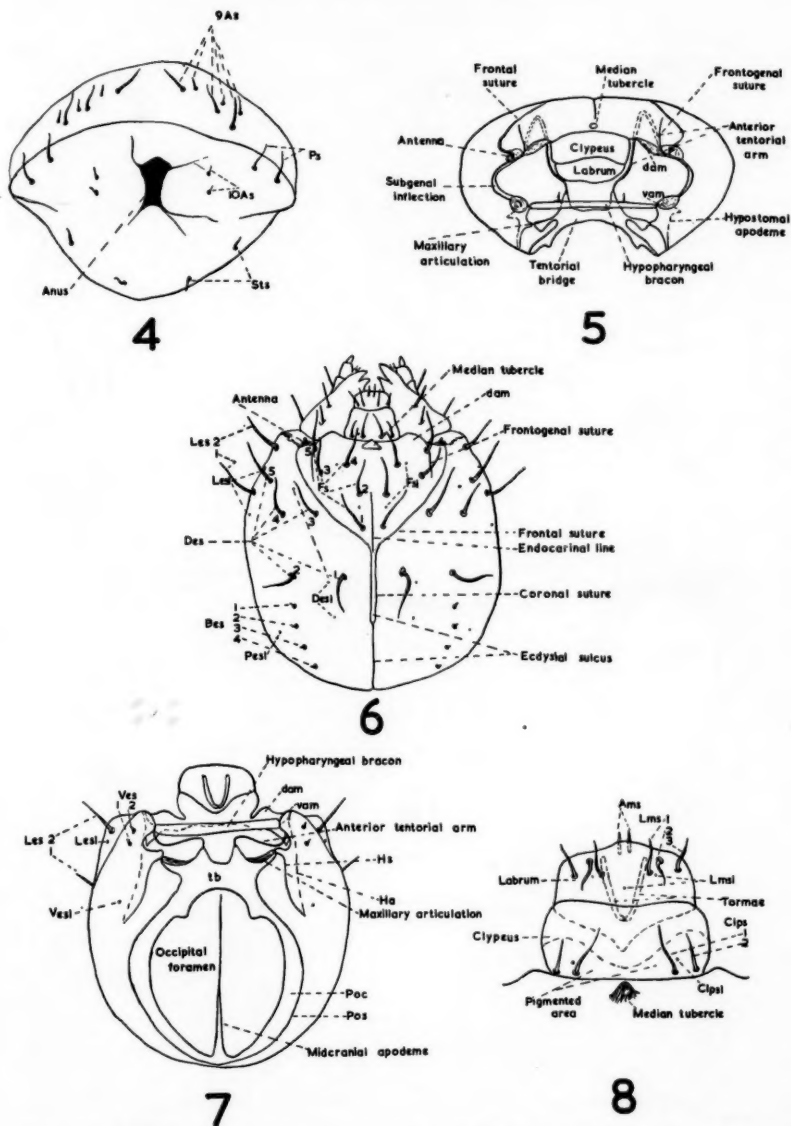
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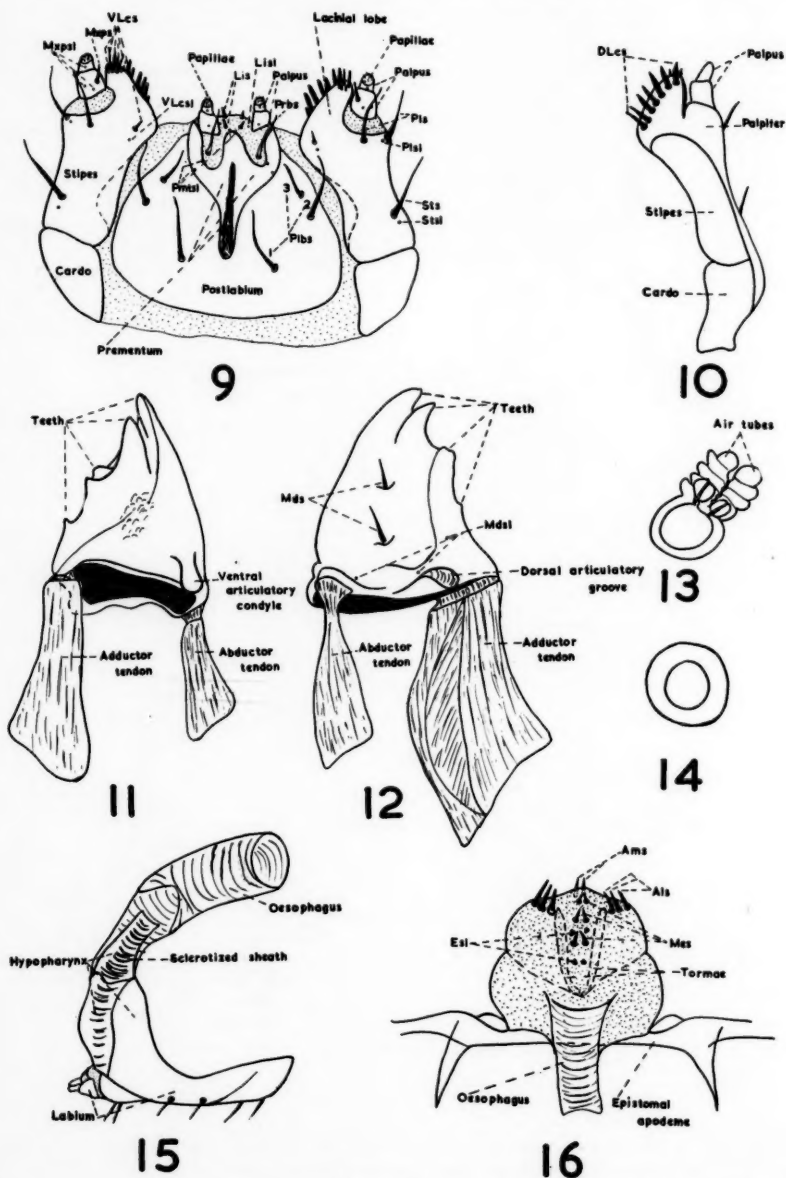
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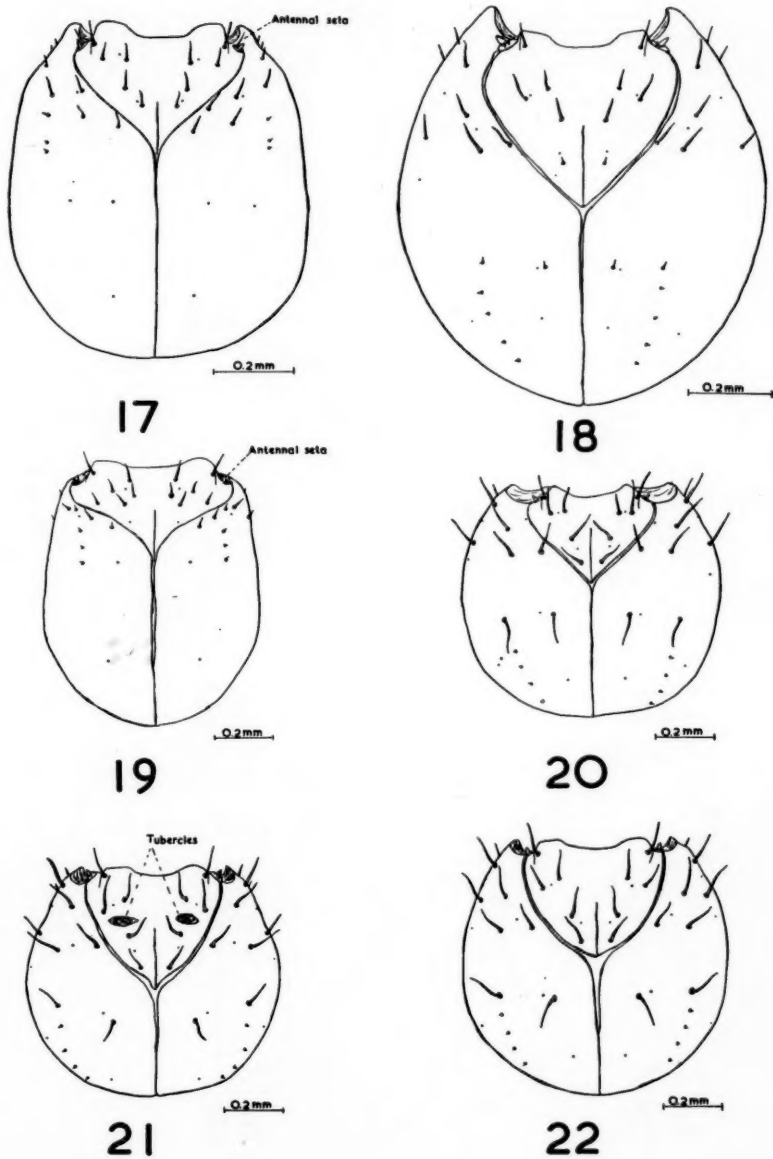
Figs. 1-3. 1, Dorsal aspect of larva of *Hylurgops pinifex*; 2, Lateral aspect of larva of *Hylurgops pinifex*; 3, Ventral aspect of larva of *Hylurgops pinifex*. As, Alar setae; AIs, Setae of abdominal segment, fold I; AIIIs, Setae of abdominal segment, fold III; 1Ts, Prothoracic dorsal setae; 2TIs, Dorsal setae of mesothorax, fold I; 2TIIIs, Dorsal setae of mesothorax, fold II; 3TIs, Dorsal setae of metathorax, fold I; 3TIIIs, Dorsal setae of metathorax, fold II; 9As, Dorsal setae of 9th abdominal segment; 10As, Dorsal setae of 10th abdominal segment; Lsts, Laterosternal setae; Msts, Mediosternal setae; Peds, Setae of pedal lobes of thorax; Ps, Pleural setae; Sps, Spiracular setae; Sts, Sternal setae; Vpls, Ventropleural setae.



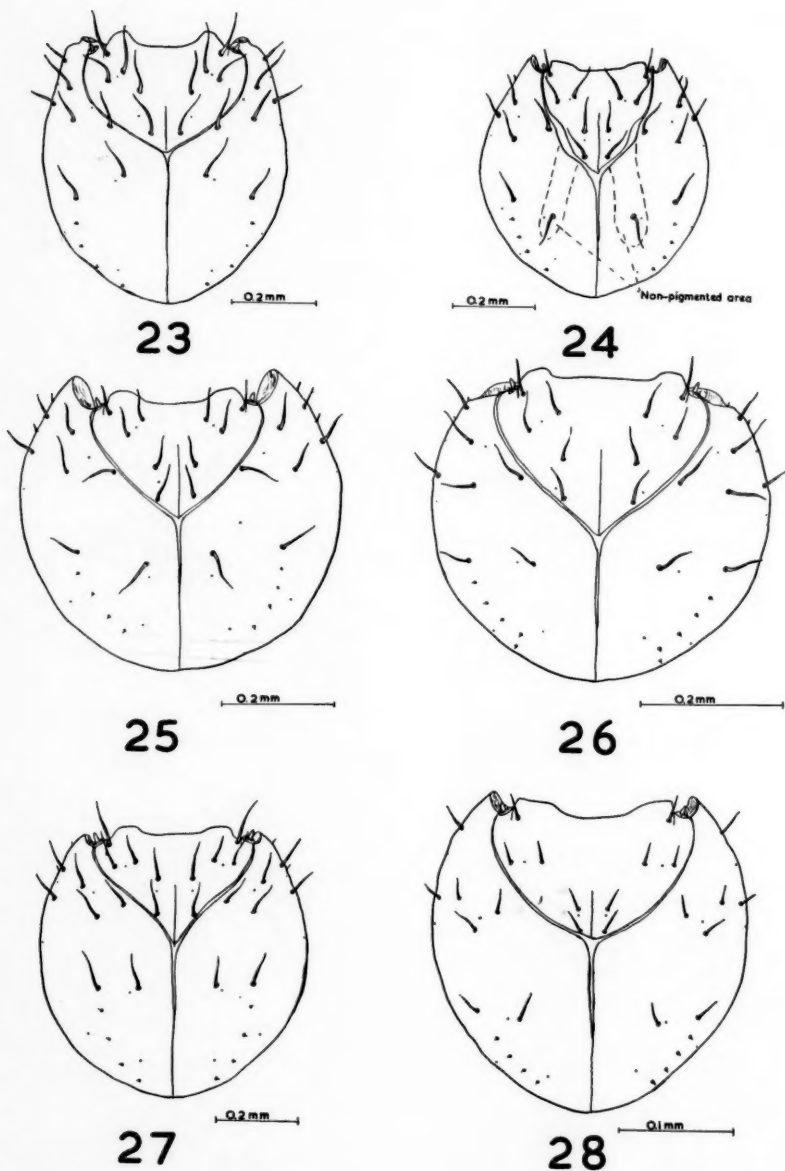
Figs. 4-8. 4, Posterior aspect of segments 9 and 10 of *Hylurgops pinifex*; 5, Anterior aspect of head capsule of *H. pinifex*; 6, Dorsal aspect of head capsule of *H. pinifex*; 7, Ventral aspect of head capsule of *H. pinifex*; 8, Dorsal aspect of labrum and clypeus of *H. pinifex*. 9As, Setae of 9th abdominal segment; 10As, Setae of 10th abdominal segment; Ams, Antero-medial setae; Clps, Clypeal setae; Clpsl, Clypeal sensilla; dam, Dorsal articulatory process of mandible; Des, Dorsal epicranial setae; Desl, Dorsal epicranial sensilla; Fs, Frontal setae; Fsl, Frontal sensilla; Ha, Hypostomal apodeme; Hs, Hypostomal suture; Les, Lateral epicranial setae; Lesl, Lateral epicranial sensilla; Lms, Labral setae; Lmsl, Labral sensilla; Pes, Posterior epicranial setae; Pesl, Posterior epicranial sensilla; Poc, Postoccipt; Pos, Postocciptal suture; Ps, Pleural setae; Sts, Sternal setae; tb, tentorial bridge; Ves, Ventral epicranial setae; Vesl, Ventral epicranial sensilla; Vam, Ventral articulation of mandible.



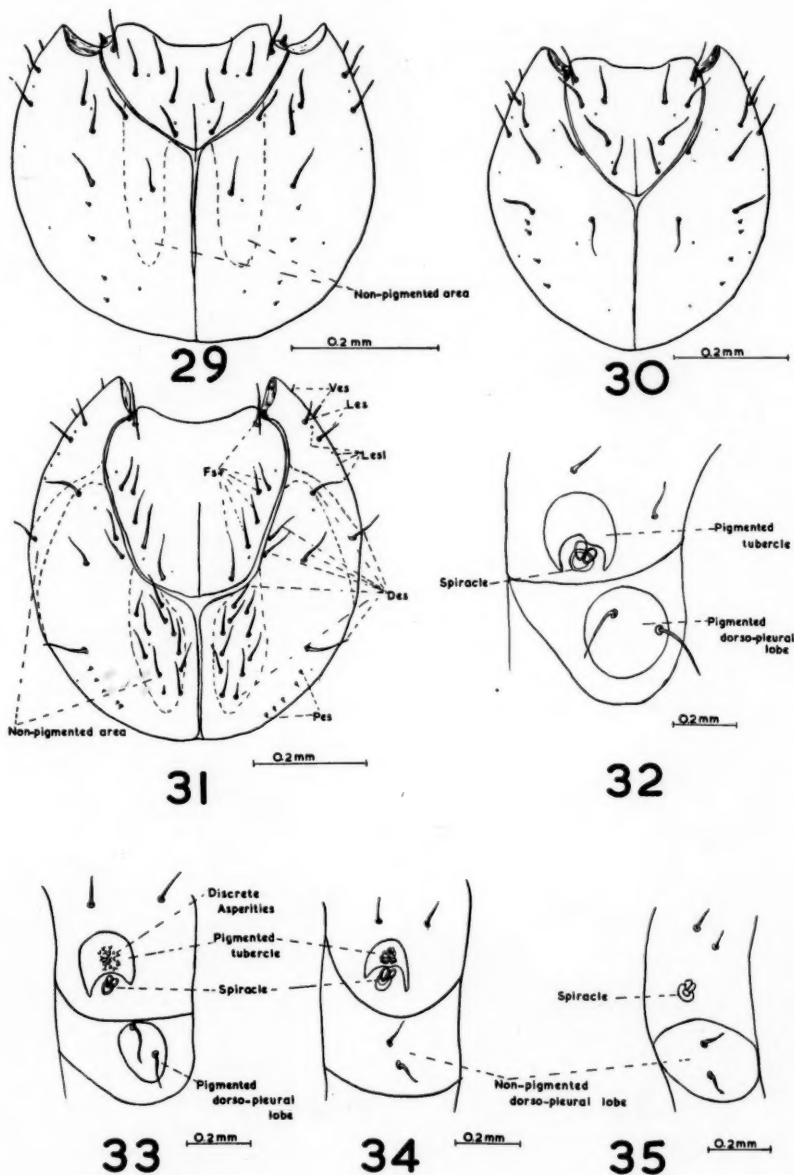
Figs. 9-16. 9, Ventral aspect of labium and maxillae of *Hylurgops pinifex*; 10, Dorsal aspect of maxilla of *Hylurgops pinifex*; 11, Ventral aspect of left mandible of *H. pinifex*; 12, Dorsal aspect of left mandible of *H. pinifex*; 13, Abdominal spiracle of *H. pinifex*; 14, Abdominal spiracle of *Pbloeosinus canadensis*; 15, Lateral aspect of hypopharynx of *H. pinifex*; 16, Epipharyngeal lining of *H. pinifex*. Als, Antero-lateral setae; Ams, Antero-medial setae; DLcs, Dorsal lacinial setae; Esl, Epipharyngeal sensilla; Lis, Ligular setae; Lisl, Ligular sensilla; Mds, Mandibular setae; Mdsl, Mandibular sensilla; Mes, Median epipharyngeal setae; Mxps, Seta on maxillary palpus; Mxpsl, Sensillae on maxillary palpus; Plbs, Postlabial setae; Pls, Palpifer setae; Plsl, Palpifera sensilla; Pmtsl, Premental sensilla; Prbs, Prelabial setae; Sts, Stipital seta; Stsl, Stipital sensilla; VLcs, Ventral lacinial setae; VLsl, Ventral lacinial sensilla.



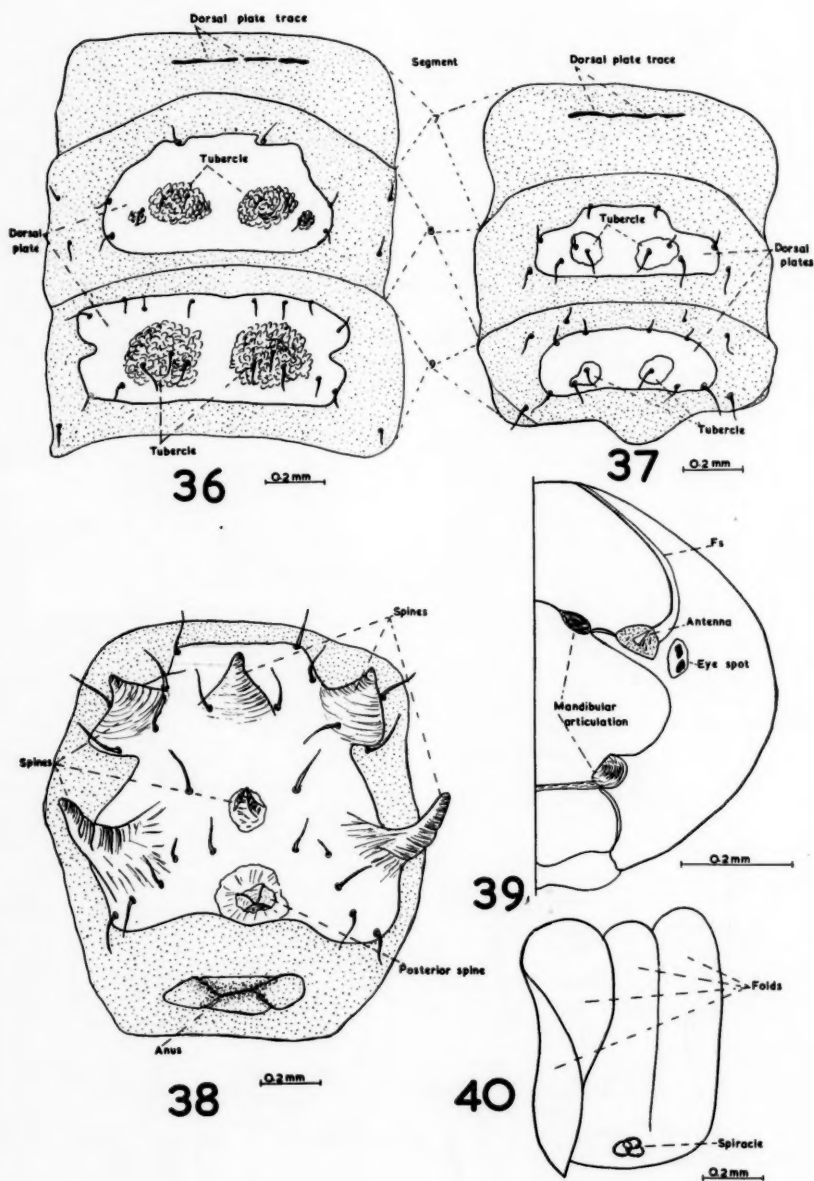
Figs. 17-22. Dorsal aspect of head capsule of: 17, *Phloeosinus canadensis*; 18, *Trypodendron lineatum*; 19, *Scolytus piceae*; 20, *Orthotomicus caelatus*; 21, *Ips pini*; 22, *Ips perturbatus*.



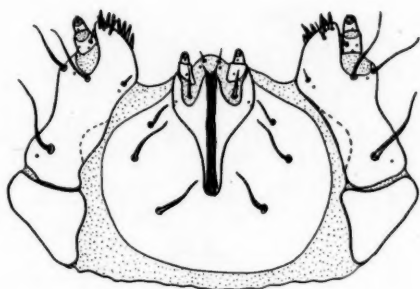
Figs. 23-28. Dorsal aspect of head capsule of: 23, *Dendroctonus piceaperda*; 24, *Pityokteines sparsus*; 25, *Pityogenes hopkinsi*; 26, *Dryocoetes affaber*; 27, *Polygraphus rufipennis*; 28, *Crypturgus atomus*.



Figs. 29-35. Dorsal aspect of head capsule of: 29, *Pityophthorus consimilis*; 30, *Conophthorus resinosae*; 31, *Gnathotrichus materiarius*. Part of a segment showing the arrangement of the spiracle in: 32, *Dendroctonus valens*; 33, *Dendroctonus rufipennis*; 34, *Dendroctonus piceaperda*; 35, *Dendroctonus simplex*. Des, Dorsal epicranial setae; Fs, Frontal setae; Les, Lateral epicranial setae; Lesl, Lateral epicranial sensilla; Pes, Posterior epicranial setae; Ves, Ventral epicranial setae.

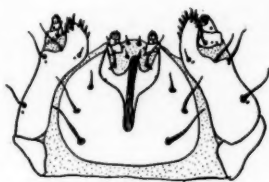


Figs. 36-40. 36, Dorsal plates on segments 7, 8 and 9 of *Dendroctonus rufipennis*; 37, Dorsal plates on segments 7, 8 and 9 of *Dendroctonus piceaperda*; 38, Dorsal plates on segments 8 and 9 of *Dendroctonus valens*; 39, Anterior aspect of left half of the head capsule of a weevil larva, *Pissodes* sp.; 40, Lateral aspect of the folds in an abdominal segment of a weevil larva, *Pissodes* sp. Fs, Frontal suture.



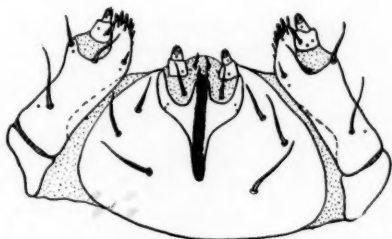
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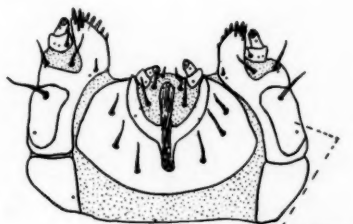
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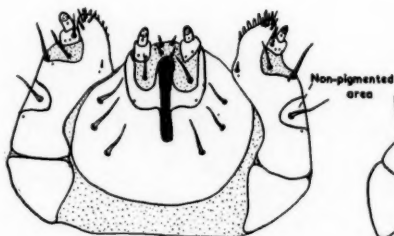
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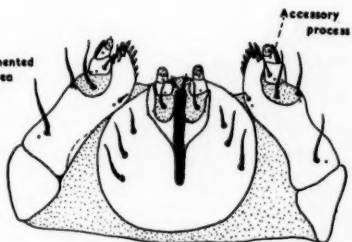
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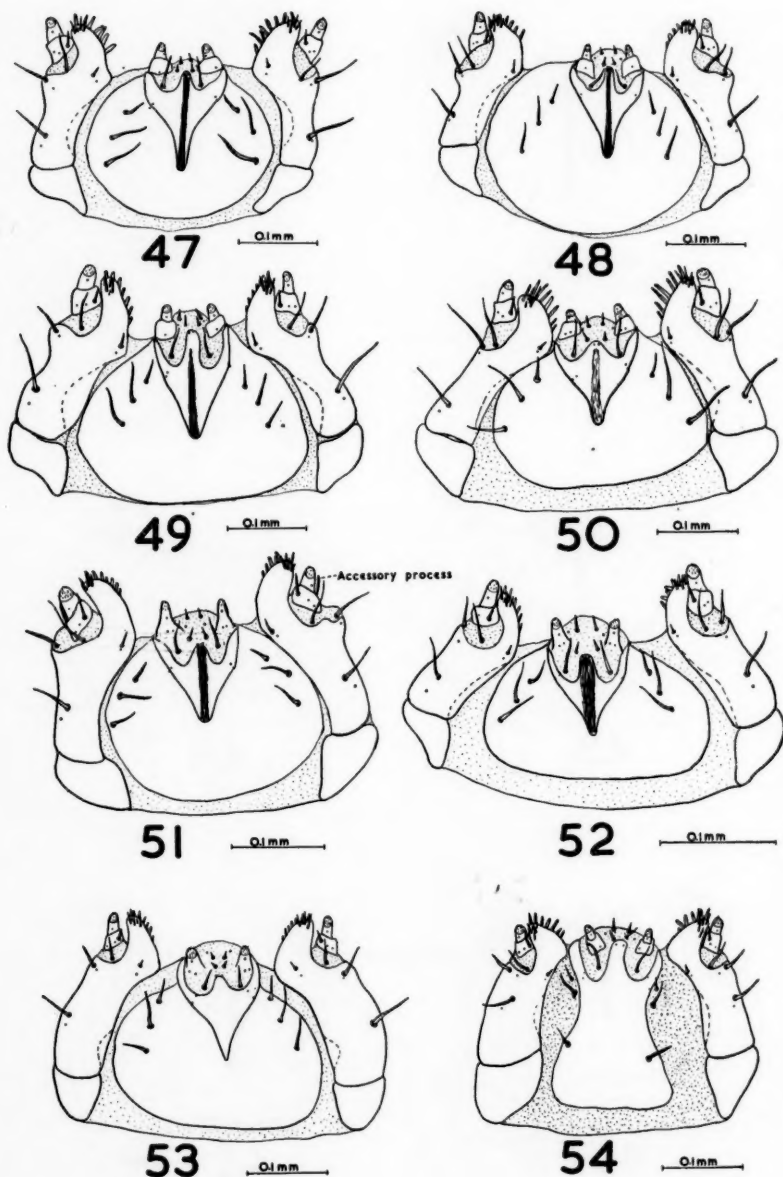


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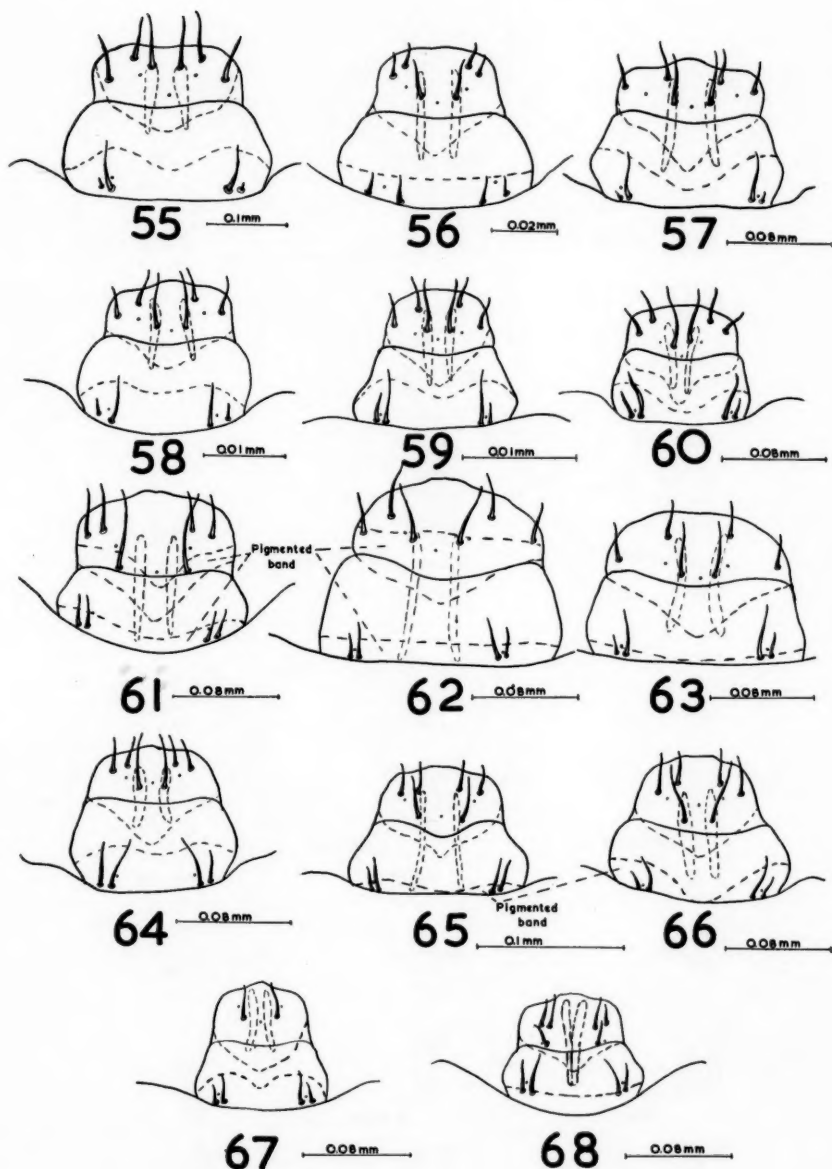
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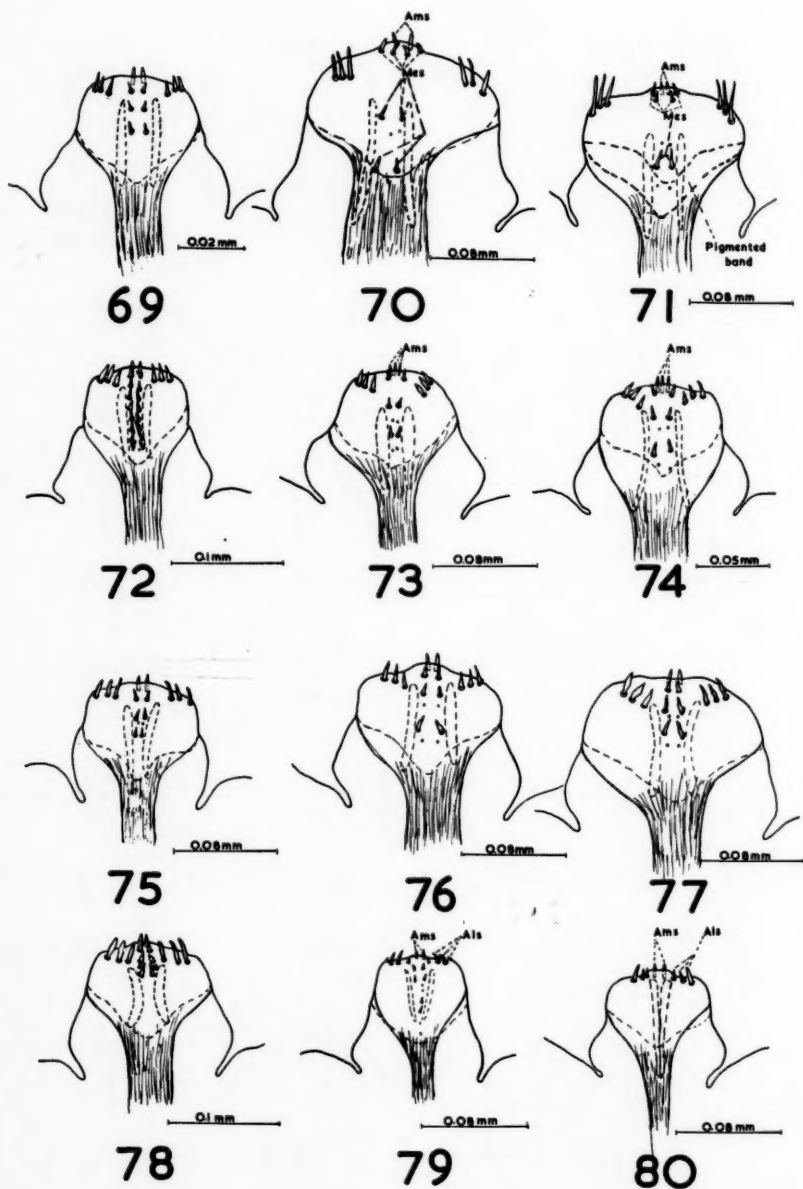
Figs. 41-46. Ventral aspect of labium and maxillae of: 41, *Dendroctonus piceaperda*; 42, *Crypturgus atomus*; 43, *Polygraphus rufipennis*; 44, *Phloeosinus canadensis*; 45, *Scolytus piceae*; 46, *Pityogenes hopkinsi*.



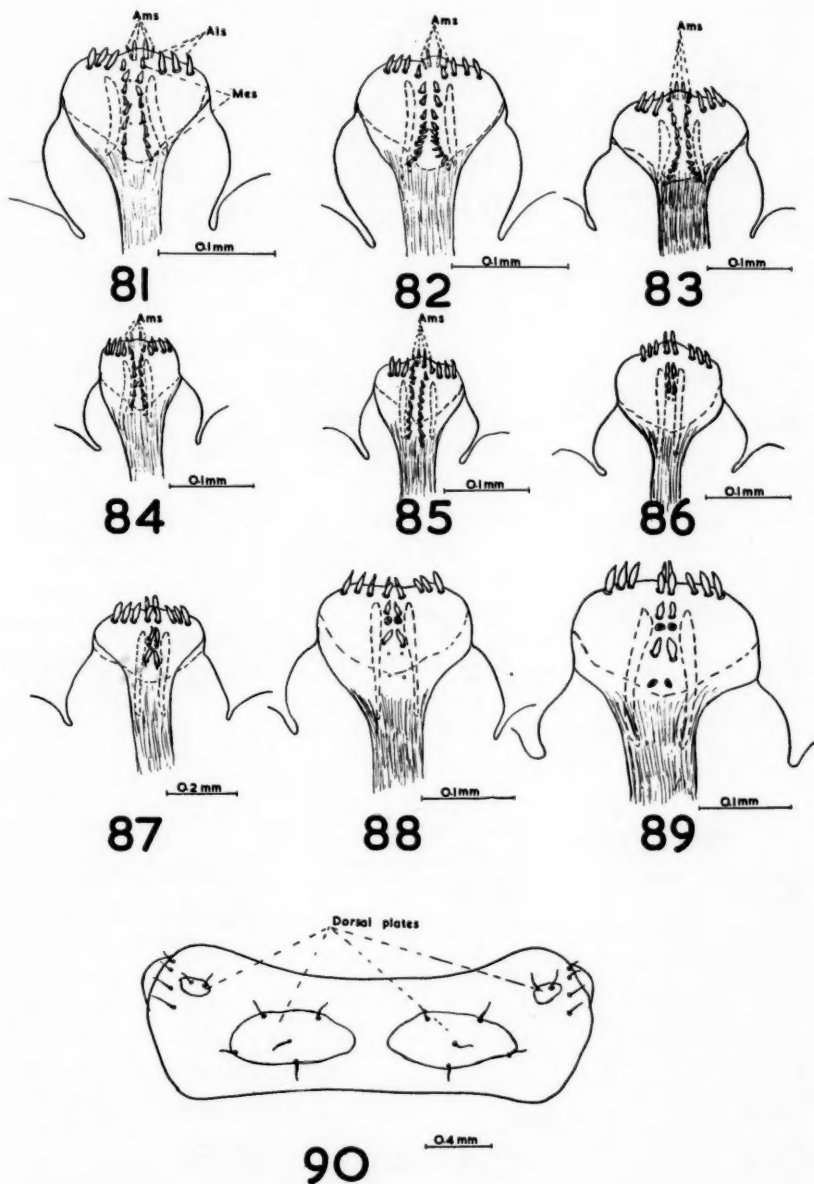
Figs. 47-54. Ventral aspect of labium and maxillae of: 47, *Orthotomicus caelatus*; 48, *Pityokteines sparsus*; 49, *Ips pini*; 50, *Dryocoetes americanus*; 51, *Conophthorus resinosae*; 52, *Pityophthorus consimilis*; 53, *Gnathotrichus materiarius*; 54, *Trypodendron lineatum*.



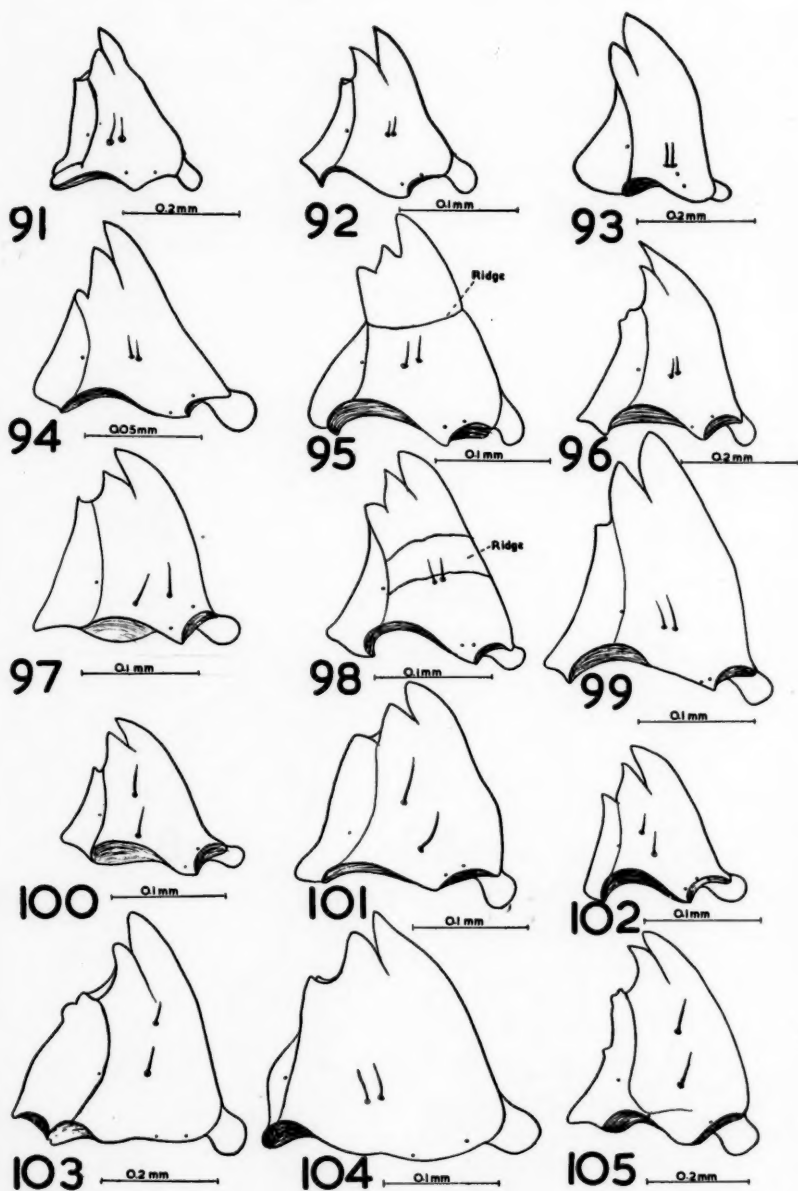
Figs. 55-68. Dorsal aspect of clypeus and labrum of: 55, *Dendroctonus rufipennis*; 56, *Crypturgus atomus*; 57, *Pityokteines sparsus*; 58, *Ips perturbatus*; 59, *Orthotomicus caelatus*; 60, *Pityogenes hopkinsi*; 61, *Phloeosinus canadensis*; 62, *Scolytus piceae*; 63, *Dryocoetes americanus*; 64, *Polygraphus rufipennis*; 65, *Pityophthorus pulchellus*; 66, *Conophthorus coniperda*; 67, *Gnathotrichus materiarius*; 68, *Trypodendron lineatum*.



Figs. 69-80. Epipharyngeal lining of labrum and clypeus of: 69, *Crypturgus atomus*; 70, *Scolytus piceae*; 71, *Pbloeosinus canadensis*; 72, *Orthotomicus caelatus*; 73, *Conophthorus coniperda*; 74, *Pityophthorus pulchellus*; 75, *Pityogenes bopkinsi*; 76, *Pityokteines sparsus*; 77, *Dryocoetes americanus*; 78, *Polygraphus rufipennis*; 79, *Gnathotrichus materiarius*; 80, *Trypodendron lineatum*. Als, Antero-lateral setae; Ams, Antero-median setae; Mes, Median epipharyngeal setae.



Figs. 81-90. Epipharyngeal lining of labrum and clypeus of: 81, *Ips pini*; 82, *Ips calligraphus*; 83, *Ips perturbatus*; 84, *Ips borealis*; 85, *Ips chagnoni*; 86, *Dendroctonus simplex*; 87, *Dendroctonus piceaperda*; 88, *Dendroctonus rufipennis*; 89, *Dendroctonus valens*, 90, Sclerotized plates on pronotum of *Dendroctonus valens*. Als, Antero-lateral setae; Ams, Antero-median setae; Mes, Median epipharyngeal setae.



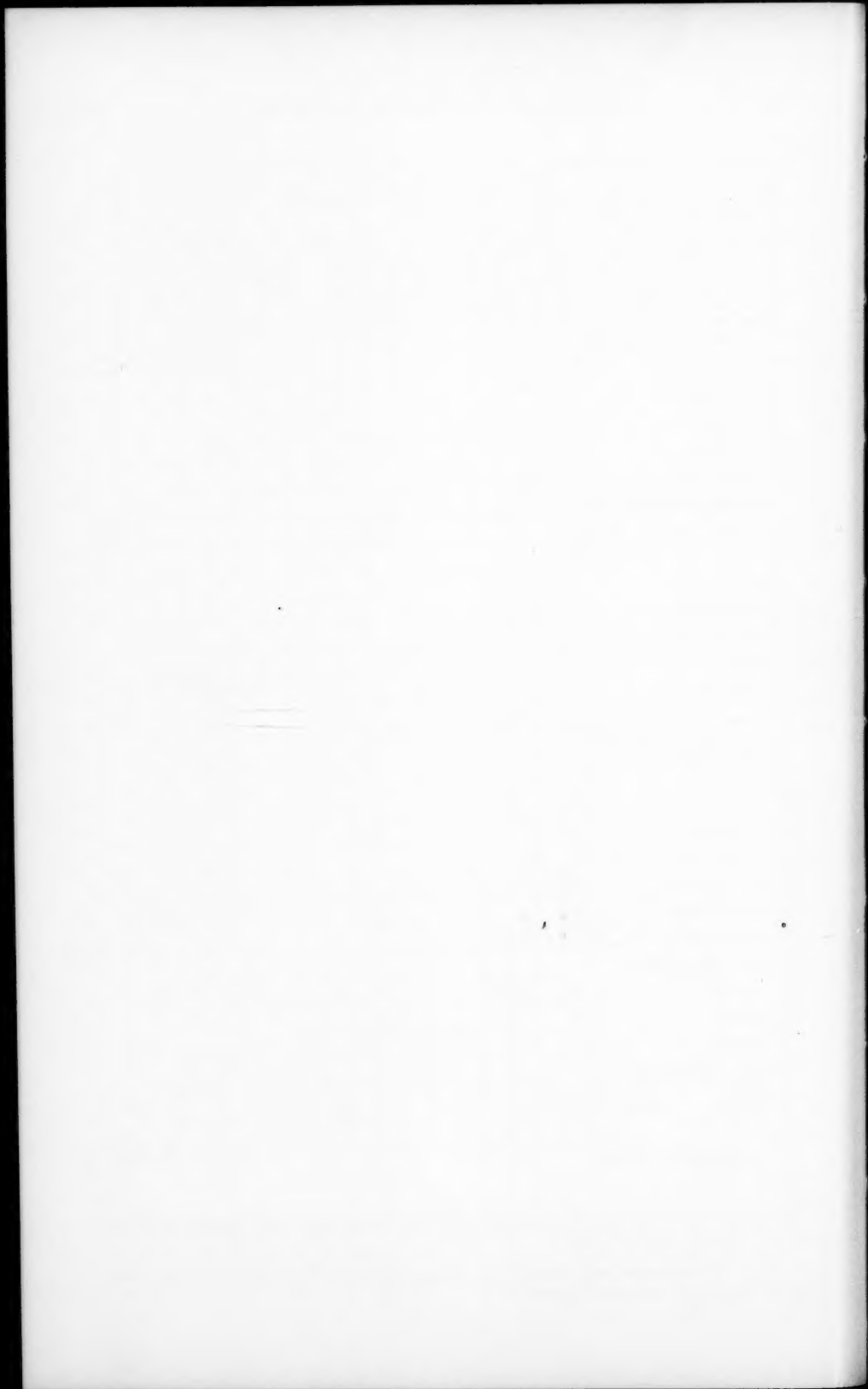
Figs. 91-105. Dorsal aspect of right mandible of: 91, *Ips pini*; 92, *Pityogenes hopkinsi*; 93, *Scolytus piceae*; 94, *Crypturgus atomus*; 95, *Polygraphus rufipennis*; 96, *Dryocoetes americanus*; 97, *Trypodendron lineatum*; 98, *Pityokteines sparsus*; 99, *Pbloeosinus canadensis*; 100, *Gnathotrichus materiarius*; 101, *Conophthorus resinosae*; 102, *Pityophthorus pulchellus*; 103, *Dendroctonus rufipennis*; 104, *Orthotomicus caelatus*; 105, *Hylurgops pinifex*.

DISTRIBUTION OF SETAE	Model No. of Setae													
	Crypturgus	Dendroctonus (4)	Hylurgops	Phloeosinus	Polygraphus	Scolytus	Conophthorus (2)	Dryocoetes (2)	Ips (5)	Orthotomicus	Pityogenes (2)	Pityokteines	Pityophthorus (6)	Trypodendron
PROTHORAX														
Dorsal	11											11-12	12	
Ventropleural lobe	2													
Mediosternal	1													
Laterosternal	3						4	4						
Pedal lobe	2	3-4	3-4	4										
MESO- & METATHORAX														
Dorsal fold I	1													4
" " II	5													
Alar area	2						3	3		3		3	4	4
Dorsopleural lobe	1													
Ventropleural lobe	1													2
Mediosternal	1												2	2
Laterosternal	3						4	4						
Pedal lobe	2	3-4	3-4	4	3									
1-8 ABDOMINAL														SEGMENT 1-7 8
Dorsal fold I	1												2	2
" " III	5													4, 2
Spiracular	2													
Dorsopleural lobe	2												1	
Ventropleural "	2							1					1	
Mediosternal	2												1	3
Laterosternal	1							2					3	
9th ABDOMINAL														
Dorsal	5	6*	6					4					3	3
Pleural	2													
Sternal	2													
10th ABDOMINAL														
Anal	2													

* *D. rufipennis* has 8

Fig. 106. Chart showing the distribution of setae on the thorax and abdomen of representatives of the 15 genera studied.

Note: A blank square indicates that the number of setae present agrees with the model number given in the left-hand column.



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**Taxonomy, Life History, and Habits of
the Elliptoid-eyed Species of *Schinia*
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by

DAVID F. HARDWICK

Insect Systematics and Biological Control Unit
Entomology Division, Ottawa, Canada

**OHIO STATE
UNIVERSITY**

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